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Rove beetles of the subtribe Scopaeina Mulsant & Rey (Coleoptera: Staphylinidae) in the West Palaearctic: Phylogeny, biogeography and species catalogue

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Abstract

A cladistic analysis of the West Palaearctic Scopaeina Mulsant & Rey, 1878 (Coleoptera, Staphylinidae: Paederinae) is presented along with bionomic and biogeographic information. A total of 76 morphological characters were coded for the 88 currently known West Palaearctic species, except for *S. bifossicapitata* (Outerelo & Oromi, 1987). Results show that Scopaeina comprises two well-supported monophyletic groups in the West Palaearctic, *Micranops* Cameron, 1913 and *Scopaeus* Erichson, 1840, which are considered to represent distinct genera. Phylogenetic relationships to *Orus* Casey, 1884, distributed in North and South America, are briefly discussed. Whereas *Micranops* is only represented by *M. pilicornis* (Baudi, 1869) in the region under study, 87 species of *Scopaeus* are currently known from the West Palaearctic. Within *Scopaeus*, the cladistic analysis yielded many well-supported monophyletic species groups, most of which are restricted to the West Palaearctic. However, except for *Hyperscopaeus* Coiffait, 1984, they are not in agreement with the widely used subgeneric concept sensu Coiffait (1952–1984). The following polyphyletic subgenera are consequently synonymized: *Alloscopaeus* Coiffait, 1968, *Anomoscopaeus* Coiffait, 1968, *Geoscopaeus* Coiffait, 1960, and *Hyposcopaeus* Coiffait, 1960 synn. n. = *Scopaeus* Erichson, 1840. *Nivorus* Herman, 1965, and *Microscopaeus* Coiffait, 1981 synn. n. = *Micranops* Cameron, 1913. The monotypical genus *Coecoscopaeus* Coiffait, 1984, established for *C. coecus* (Peyerimhoff, 1906), is excluded from Scopaeina. *Scopaeus mitratus perroti* Ochs, 1953 is raised to species rank, and *S. nigellus* Wollaston, 1864, formerly a synonym of *S. minimus* Erichson, 1939, is revalidated. Finally, we present a catalogue of species and synonyms of West Palaearctic Scopaeina along with distributional data and five new synonymies of species group names: *S. bordei* Peyerimhoff, 1914 syn. n. = *S. portai* Luze, 1910; *S. tassiliensis* Jarrige, 1958, *S. mauretanicus* Coiffait, 1960 synn. n. = *S. crassipes* Wollaston, 1867; *S. saoudiensis* Coiffait, 1981 = *S. sinaicus* Coiffait, 1970; *S. mateui* Coiffait, 1953 syn. n. = *S. didymus* Erichson, 1840. A lectotype is designated for *S. didymus* Erichson, 1840.

Key words: Staphylinidae, *Scopaeus*, *Coecoscopaeus*, *Micranops*, *Orus*, West Palaearctic, cladistics, biogeography, catalogue

See also Electronic Supplement (Parts 1–3) at **http://www.senckenberg.de/odes/02-02.htm**

Introduction

With over 45,700 nominal species rove beetles or staphylinids probably constitute the most species-rich group of Coleoptera (Smetana & Herman 2001). The family includes some very large genera with externally similar species. These genera often have a confused taxonomic history and are in need of critical revision. One of these groups is the subtribe Scopaeina Mulsant & Rey, 1878 of the paederine group, tribe Paederini, which is traditionally defined by the four-toothed labrum (e.g. Coiffait 1982, 1984). *Scopaeus*, with about 400 described species world-wide (Frisch 1997c), is the largest genus in the subtribe. The predominantly riparian beetles are small and range from 2–4 mm in length. The taxonomy of the West Palaearctic *Scopaeus* has been treated recently by Frisch (1994–2001). The present paper examines the phylogenetic relationships of the West Palaearctic members of the subtribe, testing in particular the validity of subgenera and informal species groups

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proposed by various authors, discusses biogeographic aspects, and summarises taxonomic and distributional data in a catalogue.

Taxonomic history

Erichson (1840) erected *Scopaeus* for several species which were originally described in other staphylinid genera, mainly based on mouthpart characters: dentate labrum, acute ultimate segment of maxillary palpi, and strongly sclerotised and tridentate ligula. The oldest species now referred to *Scopaeus* is *Paederus laevigatus* Gyllenhal, 1827. The first monograph of European *Scopaeus* was provided by Mulsant & Rey (1854) who described some widespread European species. Binaghi (1935), describing some South European taxa, first used the aedeagus for species definition. Coiffait (1952, 1953, 1960, 1968, 1969, 1970, 1971, 1973, 1976, 1981, 1984), who extensively published on the genus, caused much taxonomic confusion in misjudging variability and significance of external morphological characters and, hence, producing numerous synonyms at the species level. In addition, Coiffait (1952, 1960, 1968, 1981, 1984) and others introduced a series of subgenera which do not represent monophyletic groups (Frisch 1997c). Exceptions are *Micranops* Cameron and *Hyperscopaeus* Coiffait. Frisch (1994–1999c) introduced informal species groups whose monophyly will be tested here.

Micranops, also a member of Scopaeina, resembles *Scopaeus* in the four-dentate labrum and the narrow neck. It differs in the (probably plesiomorphic) structure of the aedeagus (Figs. 4–6) and in the distinct setiferous furrow behind the eyes (Figs. 1a, b), most probably an autapomorphy. *Micranops pilicornis* is the only West Palaearctic species of the genus.

The revision of material of most major collections, including relevant types, and specific collecting especially in the eastern Mediterranean provides the base for a sound taxonomic concept of the West Palaearctic members of the subtribe Scopaeina published by Frisch (1994–2001). The taxonomic revision of 114 species group names, 88 of which being considered to represent valid species, yielded 35 new synonyms and four species to be revalidated. Additionally, 31 new species were discovered. After the revision, Scopaeina comprises *Micranops pilicornis* (Baudi, 1869) and 87 species of *Scopaeus* Erichson, 1840 in the West Palaearctic, four of which have not yet been described. Taxonomic stability was increased also by designation of numerous lectotypes, and for the first time all known West Palaearctic species can be identified. Despite this dramatic increase in knowledge, additional taxa are expected mostly from the southern part of the region.

Biology and ecology

Little is known about ecology, habitat requirements and phenology of *Scopaeus* species. Available information relates mostly to Central European (e.g. Bohac 1985; Frisch 1997c, 1998; Horion 1965; Koch 1989) or East Mediterranean species (e.g. Frisch 1997c, 1998, 1999–1999d). Most *Scopaeus* species are found under stones or in gravel on damp, sandy soil of banks of both large rivers and streams, which are more or less exposed to sun and covered with organic litter and sparse pioneer vegetation. They are, however, absent from sterile, coarse gravel near the waterline. *Scopaeus* populations frequently colonise very narrow banks not wider than 10 cm, or small, suitable zones within large banks. In general, the genus can be termed ripicolous and hygro-thermophilous. *Scopaeus* species are collected from sea level up to over 2000 m. The occurrence of *Scopaeus* species depends more on the availability of suitable habitat structures near flowing waters than on altitude. Like most stenotopic riparian animals, *Scopaeus* species are increasingly endangered through habitat destruction.

Some Central European species differ in their habitat requirements from other congeners. *Scopaeus minimus* is a paludicolous humicolous species, known from marshy grounds such as wet meadows, swamps, bogs and even woods (Bohac 1985, Horion 1965, Koch 1989). *Scopaeus sulcicollis* and *S. minutus* are less hygrophilous, occuring also in barrens, grassland and forest steppes (Bohac 1985, Horion 1965, Koch 1989). In Hesse (Germany), *S. sulcicollis* was frequently found in relatively dry grassland such as *Brometalia erecti* or *Arrhenatheretum elatioris* (J. Frisch, pers. observation).

Nothing is known about feeding habits, and neither larval instars nor larval habitat requirements have been described (Coiffait 1984). Frank (1982) and Santamaria (1997) reported Neotropic, Oriental and Palaearctic *Scopaeus* species as hosts of parasitic ascomycetes.

Material and methods

Abbreviations, conventions and definitions

Over 10,000 specimens of West Palaearctic *Scopaeus* were examined, including available types. Depositories are cited as follows:

BMNH = Natural History Museum, London; DEIC = Deutsches Entomologisches Institut, Eberswalde; FMNH = Field Museum of Natural History, Chicago; HECO = Hope Entomological Collections, Oxford; HKCB = Horst Korge Private Collection, Berlin; HNHM = Hungarian Natural History Museum, Budapest; ISNB = Institut Royal des Sciences Naturelles de Belgique, Brussels; JFCG = Johannes Frisch Private Collection, Gießen; MCSN = Museo Civico di Storia Naturale

„Giacomo Doria“, Genova; MHNG = Muséum d'histoire naturelle, Genève; MHNL = Musée Guimet d'histoire naturelle, Lyon; MLZT = Museo di Zoologia Sistematica della Universita, Turin; MNHN = Muséum National d'Histoire Naturelle, Paris; MZKI = Zoological Museum, Kiew; MZLU = Zoological Museum, Lund; MZMC = Zoological Museum, Moscow; NHMB = Naturhistorisches Museum, Basel; NHMW = Naturhistorisches Museum, Wien; NMPC = Národni Muzeum, Prague; SMNS = Staatliches Museum für Naturkunde, Stuttgart; SMTD = Staatliches Museum für Tierkunde, Dresden; ZMAL = Zoological Museum, Academy of Sciences, St. Petersburg; ZMHB = Museum für Naturkunde, Berlin; ZSMC = Zoologische Staatssammlung, München.

The aedeagus of most males was examined, and, as far as possible, terminal sclerites and spermathecae of at least ten females per species were dissected. The male of *S. nigellus* and the females of *S. binaghii*, *S. fageli*, *S. hercegovinensis*, *S. mariae*, *S. persicus*, *S. pusilloides*, *S. schillhammeri*, and *S. subopacus* remain unknown.

The count of abdominal sternites and tergites corresponds to the number of morphological rather than visible segments. Measurements were taken using a stereo dissecting microscope (Olympus SZH10) with an eye-piece linear micrometer and are based on at least ten specimens per species, including both sexes. Both eye length and temporal length are measured in lateral view. Antennal segments are measured excluding the basal and distal tapering portion. The genital terminology is taken from Blackwelder (1936), Lindroth (1957), Naomi (1990) and Frisch (1994), that of the genital sclerites from Uhlig (1989). The spermathecal terminology follows Frisch (1996, 1997c): 'chamber' refers to the lumen from which the spermathecal duct arises, 'process' is used for the solid portion. Aedeagus, spermatheca and terminal sclerites were drawn from glycerin mounts using a compound microscope (Olympus BX 40) with the drawing attachment U-DA. Aedeagi had been cleared in dioxan for several days.

The zoogeographic region covered here comprises the western part of the Palaearctic: Europe, North Africa, the northern Arabian peninsula and the Middle East, delimited in the South by the Tropic of Cancer and in the East at about 60° longitude.

Cladistic analysis

The cladistic analyses were performed with NONA version 2.0 (Goloboff 2000) using the heuristic search option and following settings: 5,000 random taxon addition replications (mult*N), 5 starting trees per replication, and multiple tree-bisection-reconnection (TBR) branch swapping. The NONA bootstrap consensus tree was calculated with 1,000 replications, 10 search replications (mult*N), and 5 starting trees per replication. The character matrix was manipulated with WinClada version 09.99m24 (beta) (Nixon 1999). In total 76 characters were included, 3 of which proved to be phylogenetically uninformative. The number of character states varied between 2 and 10. All characters were given equal weight and treated as unordered (non-additive). Question marks denote lacking information. WinClada was also used for mapping characters on the trees.

The analysis is restricted to West Palaearctic taxa and includes 86 (82 described + 4 undescribed) of the 87 presently known *Scopaeus* species, and one species each of *Micranops* and *Luzea* Blackwelder, 1952. The latter, another member of the tribe Paederini but subtribe Medonina Casey, 1905, served as outgroup. It was chosen for its relatively primitive aedeagal condition in which it resembles the basal *Micranops*.

The anophthalmous, endogean species *Scopaeus bifossicapitata* (Outerelo & Oromi, 1987) from the Canaries was not included in this study, because males are unknown and no specimens were available. *Scopaeus bifossicapitata* was first described as a species of *Domene*, but later transferred to *Scopaeus* by Outerelo & Gamarra (1989). *Coecoscopaeus coecus* (Peyerimhoff, 1906) from Tunisia, originally described in *Scopaeus*, is also excluded from the present study. *Coecoscopaeus* was placed by Coiffait (1984) in the subtribe Scopaeina, but differs considerably in external and aedeagal characters from the definition of Scopaeina by Coiffait (1982) which is adopted here.

Character assessment

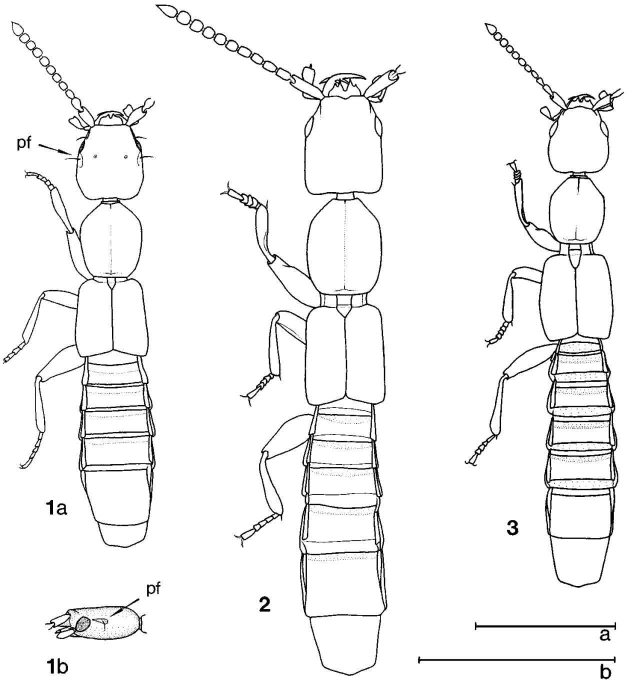
The exoskeleton of *Scopaeus* provides few distinguishing characters except for male sternite 8. The spermathecae and particularly the aedeagi, in contrast, provide many meaningful apomorphic features of high value for phylogenetic examinations on the species-group level. The mouthparts appear to be informative at the genus-group or higher level, but not for defining species or species groups. Derived characters of single species (autapomorphies) are not discussed in the present study. Characters and their character states are compiled in Appendix 1.

Exoskeleton

Descriptions of *Scopaeus* species usually contain extensive information on punctation and microsculpture of the body surface, which are similar in related species and even species groups. They are of little use for this analysis. Two fundamental groups exist: most species share rather shiny, spaciously punctate and weakly reticulate surfaces (char. 5:0). In contrast, some groups of related species, including *Luzea* and *Micranops*, have dull, very finely and densely punctate, microsculptured bodies (char. 5:1).

Scopaeus is characterized by a very narrow neck which is only from one fifth (char. 1:1) to about one eighth (char. 1:2) as wide as the head (Figs. 2, 3). In *Micranops*, the neck measures about one quarter of the head width (char. 1:1; Fig. 1a). *Luzea* has a notably broader neck (char. 1:0).

Within Paederinae, the shape of the labrum is a distinguishing character at the genus level (Coiffait 1982). Although there are some exceptions (Herman, pers.



Figs. 1–3. 1a) *Micranops pilicornis*, habitus, male – lectotype; **1b)** *M. pilicornis*, head lateral; **2)** *Scopaeus* (*Hyperscopaeus*) *spathiferus*, habitus, male – holotype; **3)** *S. kovaci*, habitus, male – paratype. Abbreviation: pf = postorbital furrow. Scale a (1 mm): Figs 1a, 1b; scale b (1 mm): Figs 2, 3.

comm.), *Scopaeus* and *Micranops* have evolved a four-toothed labrum (char. 3:1; Figs. 1–3), whereas the labrum of *Luzea* has two median teeth and is laterally rounded. This simple labrum (char. 3:0) is considered to represent the plesiomorphic state.

The head shape is not significantly variable within *Scopaeus*. Nevertheless, two major groups exist, which represent the subgenera *Scopaeus* s. str. and *Polyodontus* Solier in Gay, 1849 of ancient authors. *Scopaeus* s. str. is characterized by quadrilateral or rectangular heads with parallel temples and widely rounded hind angles (char. 6:1). *Micranops* is coded as belonging to this group. Unlike this, the heads of *Polyodontus* are more or less trapezoid with less rounded hind angles and frequently concave hind margins (char. 6:2). A third character state is coded for the very elongate, parallel heads of *Hyperscopaeus* (char. 6:0; Fig. 2). The eye length is a variable character within *Scopaeus*, which, however, seldom indicates relationships, because due to different habits obviously linked species frequently have different eye lengths. Flightless species have smaller eyes than flying ones, and endogeal species, e.g. *S. alaschiacus* from Cyprus, have strongly reduced eyes. Some species groups, however, share comparatively large eyes which are little shorter than the tempora (char. 7:1). In the present cladistic analysis, hence, these taxa are compared with the remaining species (char. 7:0).

The protarsomeres of staphylinids are frequently dilated (Uhlig 1990). This convergence is without use for this phylogenetic study. In *Scopaeus*, the protarsomeres are also dilated (chars 8:2, 8:3) but somewhat elongate (char. 8:0) or slightly transverse (char. 8:1) in few species groups. The protarsomeres of *S. portai* are transverse in the male and slender in the female, and thus even sexually dimorphic. The slender states of the protarsomeres (chars 8:0, 8:1) are considered to be plesiomorphic.

Even though the mesotibiae of *Scopaeus* species are frequently dilated, the members of the *S. sulcicollis* group (Frisch 1999b) agree in possessing remarkably dilated mesotibiae which are at least five times as wide as long (char. 9:1). These species are coded separately.

The distal antennomeres of most *Scopaeus* are more or less transverse (char. 11:2), but in some species groups they are slightly elongate (char. 11:1), and even very slender in *Hyperscopaeus* (char. 11:0). Transverse antennomeres are most likely apomorphic.

Whereas both the legs and antennae of *Scopaeus* are studded with few longer setae only, the appendages of *Micranops* and *Hyperscopaeus* bear many long, black setae (chars 10:1, 12:0). However, it remains doubtful which character state is derived, because these setae occur in many paederines.

Spermatheca

Whereas the outgroup taxa *Luzea* and *Micranops pilicornis* share the primitive one-piece spermatheca of Coleoptera (char. 13:0; Fig. 22), which was described by many authors (e.g. Heberdey 1931, de Marzo 1982), the spermathecae of all hitherto examined *Scopaeus* and the *Micranops* species illustrated by Herman (1965a) have the additional portion (char. 13:1; Figs. 23–29) described by Frisch (1996, 1997c). Because the chamber and the additional portion are connected by muscles, we interpret the two-piece spermatheca as a sperm-pump. Furthermore, except for *Hyperscopaeus* (char. 16:0; Fig. 23), the chamber of the spermatheca bears a typical process (char. 16:1; Figs. 24–29). Even though the spermathecae of *Scopaeus* species are similar and of little use for distinguishing species (Frisch 1998), the spermathecal duct and the chamber provide some characters typical for species groups. Moreover, the spermathecal duct in some species groups ends in a strongly sclerotized, bursiform structure of characteristic shape. Considering its position within the genital segments (Fig. 30), it is assumed to be the bursa copulatrix (Frisch, in press). Various character states of the spermathecal duct (char. 14), the "bursa" (char. 15) and the chamber of the spermatheca (chars 16, 17) were used for this analysis.

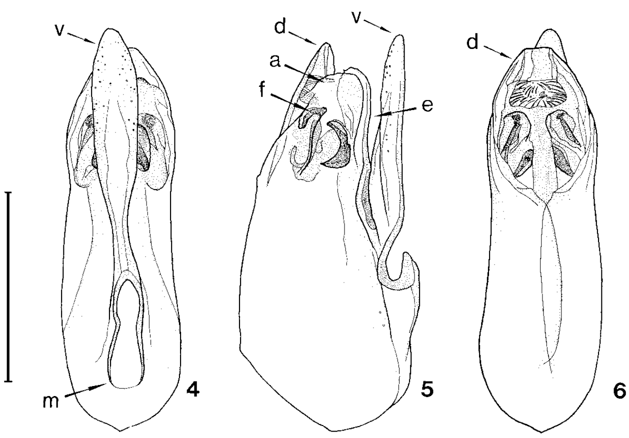
Abdominal terminal sclerites

In staphylinids, the abdominal terminal sternites of males usually provide various, frequently species-specific, secondary sexual modifications such as planations, groups of setae or distal emarginations (Blackwelder 1936, Naomi 1990). In particular, sternite 8 is strongly emarginate terminally, because the aedeagus comes out ventrally. These emarginations are rather small in *Luzea* and *Micranops* (char. 23:2; Fig. 31), but large and frequently strongly derived (Figs. 32–36) in *Scopaeus* and, hence, of high phylogenetic value. Most species, however, have a simple, triangular emargination (char. 32:0; Fig. 34), most likely the plesiomorphic character state for *Scopaeus*. Further characters are provided by the male abdominal sternite 7, which bears some thick setae in *Micranops* (char. 21:1) and has a deep, quadrilateral emargination in the *S. signifer* group (char. 21:2), and by the hind margin of the female sternite 8, which is somewhat emarginate in *Hyperscopaeus* (char. 18:1), whereas it is convex in the remaining taxa included in this study (char. 18:0).

The apex of laterotergite 9 (Figs. 37–39) provides useful characters regarding the phylogenetic relationships between Scopaeina and allied groups. In *Luzea*, it is deeply incised and extended into two teeth of equal length (char. 19:0), whereas the dorsal tooth is strongly reduced or even lacking and the sclerite thus unidentate in the examined Scopaeina (char. 19:1).

Aedeagus

Most characters used in this phylogenetic study are taken from the aedeagus. Bearing in mind the primitive type of the aedeagus of staphylinids and the Paederinae as described by Blackwelder (1936) and Naomi (1990), the aedeagi of *Scopaeus* (Figs. 7–21) appear highly derived due to the reduced median lobe, which became divided into a large, distinct dorsal lobe and two large, lateral apical lobes (Frisch 1994). *Luzea* and *Micranops* (Figs. 4–6), however, agree in rather plesiomorphic aedeagi with short such lobes (char. 26:0) but with an additional, remarkable ventral lobe (char. 33:1) which is found in many paederines. This ventral lobe is part of the median lobe and was erroneously considered to represent ventro-medially fused parameres (Herman, pers. comm.). Unlike this, the large aedeagi of *Hyperscopaeus* (Figs. 7–9) are quite different, because the feebly sclerotized distal portion of the long median lobe (char. 26:1) bears distinct lobes only at the very end (char. 57:0). Character states for parts of the aedeagi are compiled in Appendix 1, but major characters are described below.



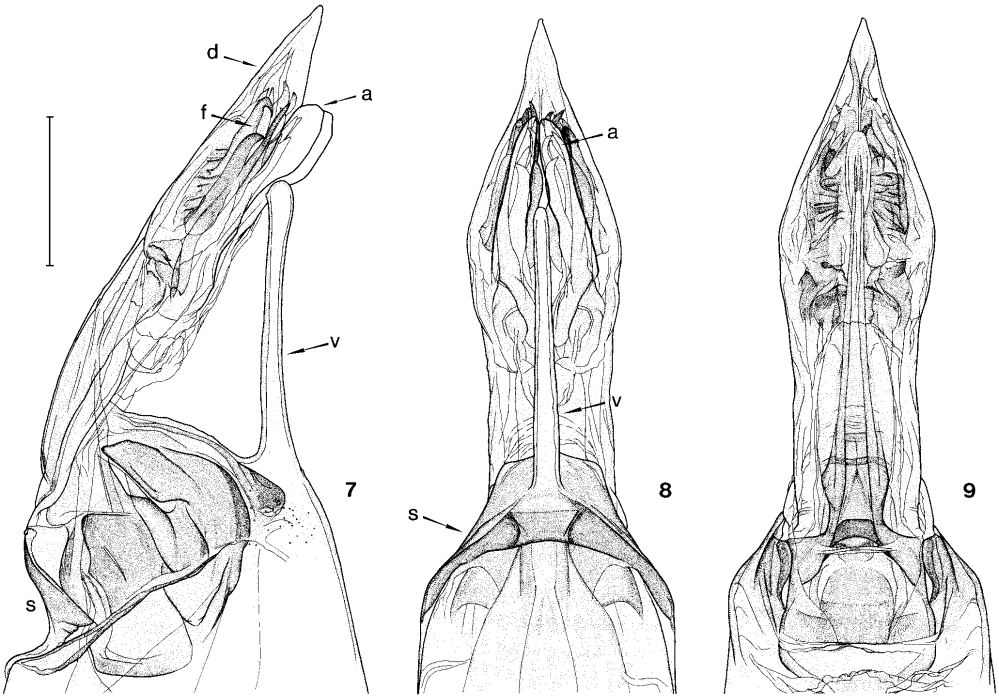
Figs. 4–6. *Micranops pilicornis*, lectotype, aedeagus in 4) ventral, 5) lateral, 6) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, m = median foramen, v = ventral lobe of median lobe. Scale = 0.1 mm.

Following Blackwelder (1936), the sclerotized end of the ejaculatory duct is termed the flagellum. Whereas the flagellum is long and surrounded by various tooth-like structures in *Hyperscopaeus* (char. 28:0; Figs. 7–9), it is stout in *Micranops* (char. 28:2; Figs. 4–6) and *Luzea* (char. 28:1), though surrounded by teeth in the latter. Unlike this, the flagellum of *Scopaeus* s. str. is more or less lengthened and of variable shape (char. 28:3; Figs. 7–21), frequently specific for species groups.

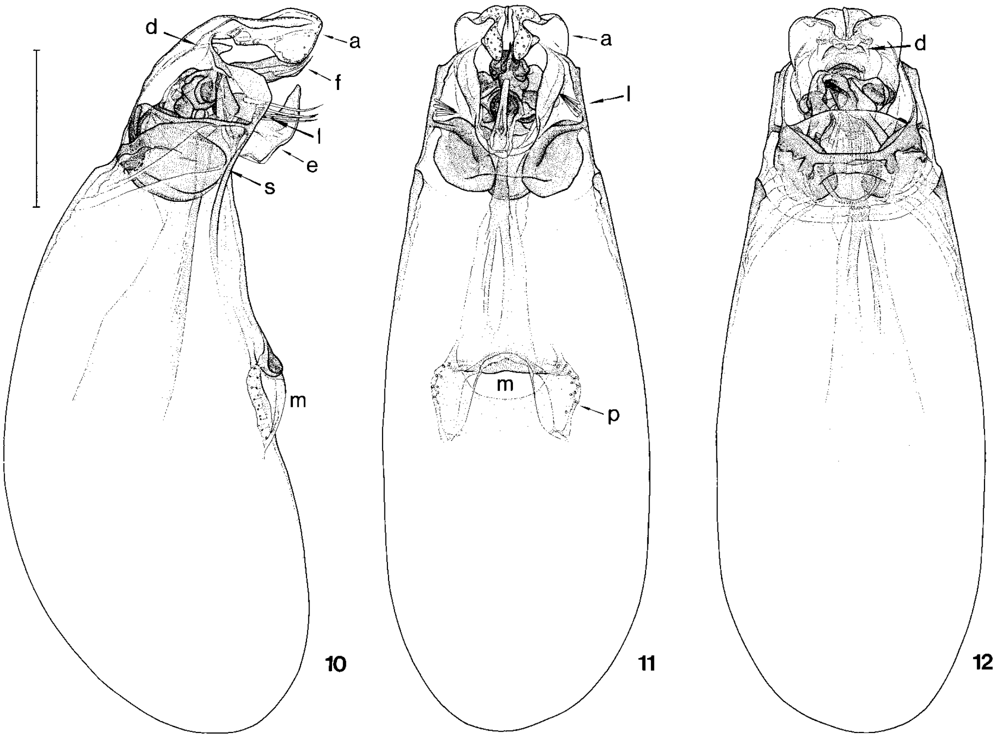
According to Coiffait (1982), the subtribe Scopaeina lacks distinct parameres. However, the parameres are represented in *Scopaeus* and the New World genus *Orus* and in many other paederines by strongly reduced lobes of varying lengths and widths appressed to the median lobe near the median foramen (Figs. 7–21) (Herman, pers. comm.) The so-called lateral lobes (e.g. Coiffait 1982, Frisch 1994) of *Scopaeus* (chars 39:1–9; Figs. 7–21) are not parameres but lobes of the median lobe (Herman, pers. comm.). These variable lobes are reduced in many groupings or even lacking and provide valuable characters for this study.

The aedeagus of *Scopaeus* bears a variable ventral process of the endophallic structures (char. 35:1), which provides derived characters specific for species groups. For example, the *S. elegans* group (Frisch 1994) has a flagellate process (char. 36:5; Figs. 19, 20), and in the species allied to *S. didymus* it is short and hook-shaped (char. 36:4). This endophallic process, however, is absent in the outgroup and some basal groups of *Scopaeus* (char. 35:0).

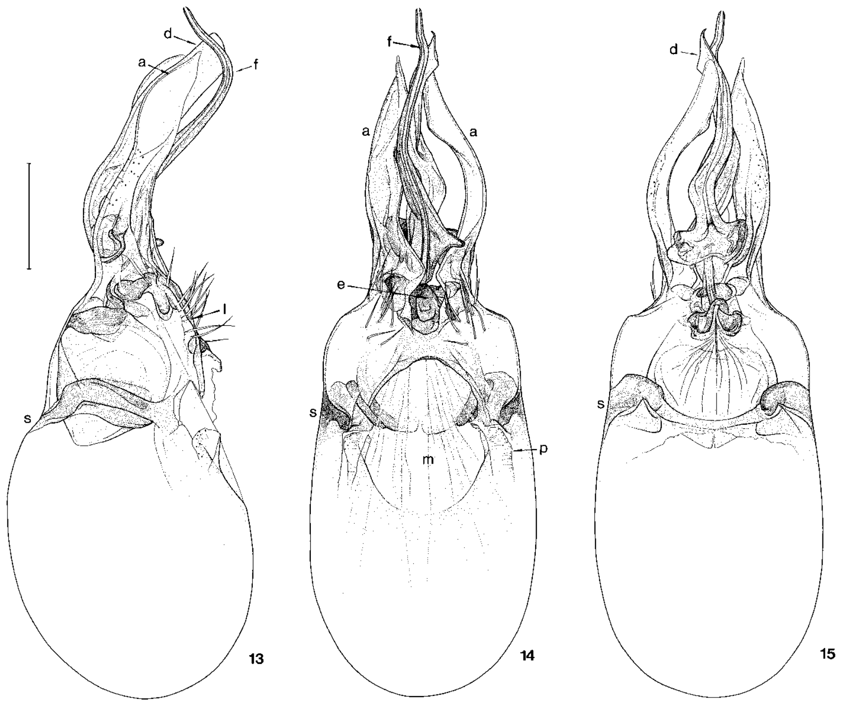
Except for the outgroup, *Micranops* and *Hyperscopaeus*, *Scopaeus* species agree in the presence of testaceous, ventrally more or less enlarged apical lobes (char. 58:2; Figs. 10–21) which provide striking apomorphic characters for both species and species groups. These apical lobes, however, are rather simple in the *S. debilis* (Frisch 1999), the *S. longicollis* (Frisch 1999c), and the *S. signifer* (Frisch 1997c) groups (Figs. 10–12).



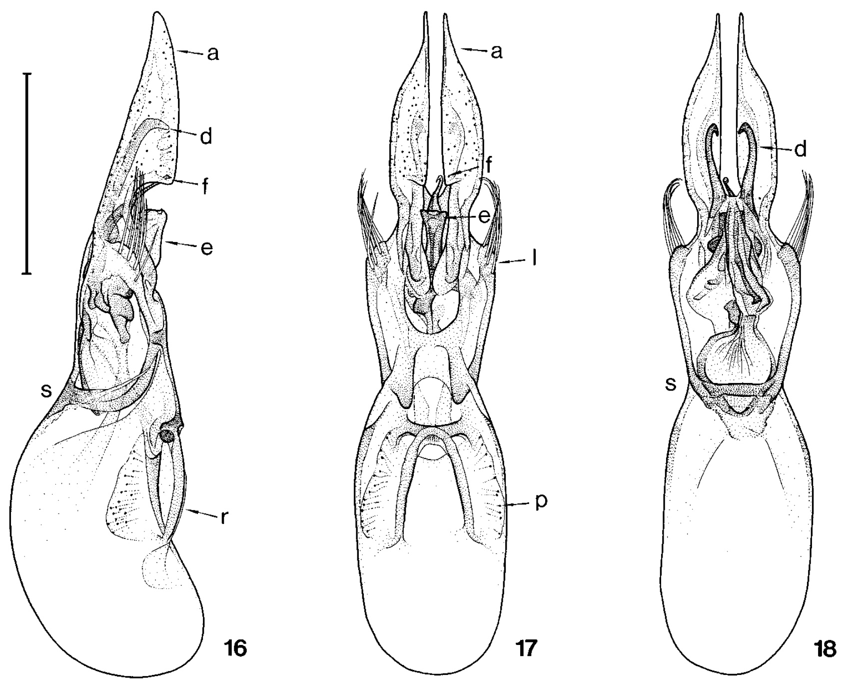
Figs. 7–9. *Scopaeus* (*Hyperscopaeus*) *spathiferus*, holotype, aedeagus in 7) lateral, 8) ventral, 9) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, f = flagellum, s = sclerotized ring of phallobase, v = ventral process of phallobase. Scale = 0.1 mm.



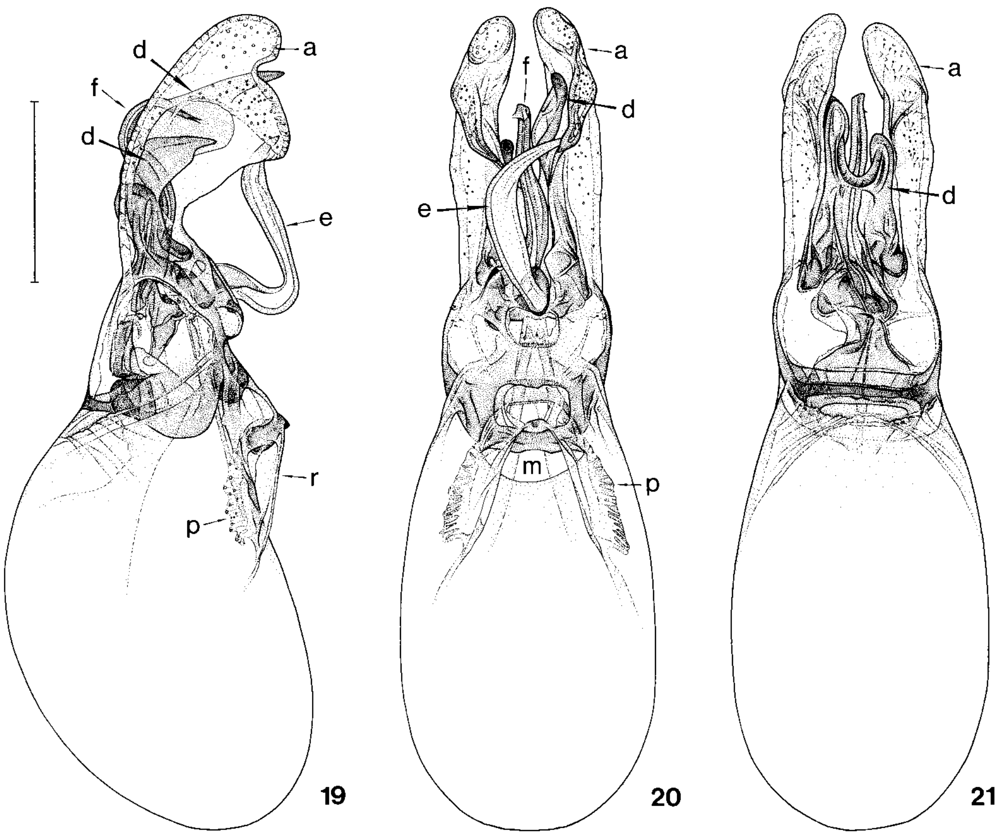
Figs. 10–12. *Scopaeus debilis* (*S. debilis* group), Tunisia, Kasserine, aedeagus in 10) lateral, 11) ventral, 12) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, l = lateral lobe, m = median foramen, p = paramere, s = sclerotized ring of phallobase. Scale = 0.1 mm.



Figs. 13–15. *Scopaeus siculus* (*S. gracilis* group), lectotype, aedeagus in 13) lateral, 14) ventral, 15) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, l = lateral lobe, m = median foramen, p = paramere, s = sclerotized ring of phallobase. Scale = 0.1 mm.



Figs. 16–18. *Scopaeus alaschiacus* (*S. minutus* group), holotype, aedeagus in 16) lateral, 17) ventral, 18) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, l = lateral lobe, p = paramere, r = lateral ridges of median foramen, s = sclerotized ring of phallobase. Scale = 0.1 mm.



Figs. 19–21. *Scopaeus kurdistanicoides* (*S. elegans* group), holotype, aedeagus in 19) lateral, 20) ventral, 21) dorsal view. Abbreviations: a = apical lobe, d = dorsal lobe, e = ventral endophallic process, f = flagellum, m = median foramen, p = paramere, r = lateral ridges of median foramen. Scale = 0.1 mm.

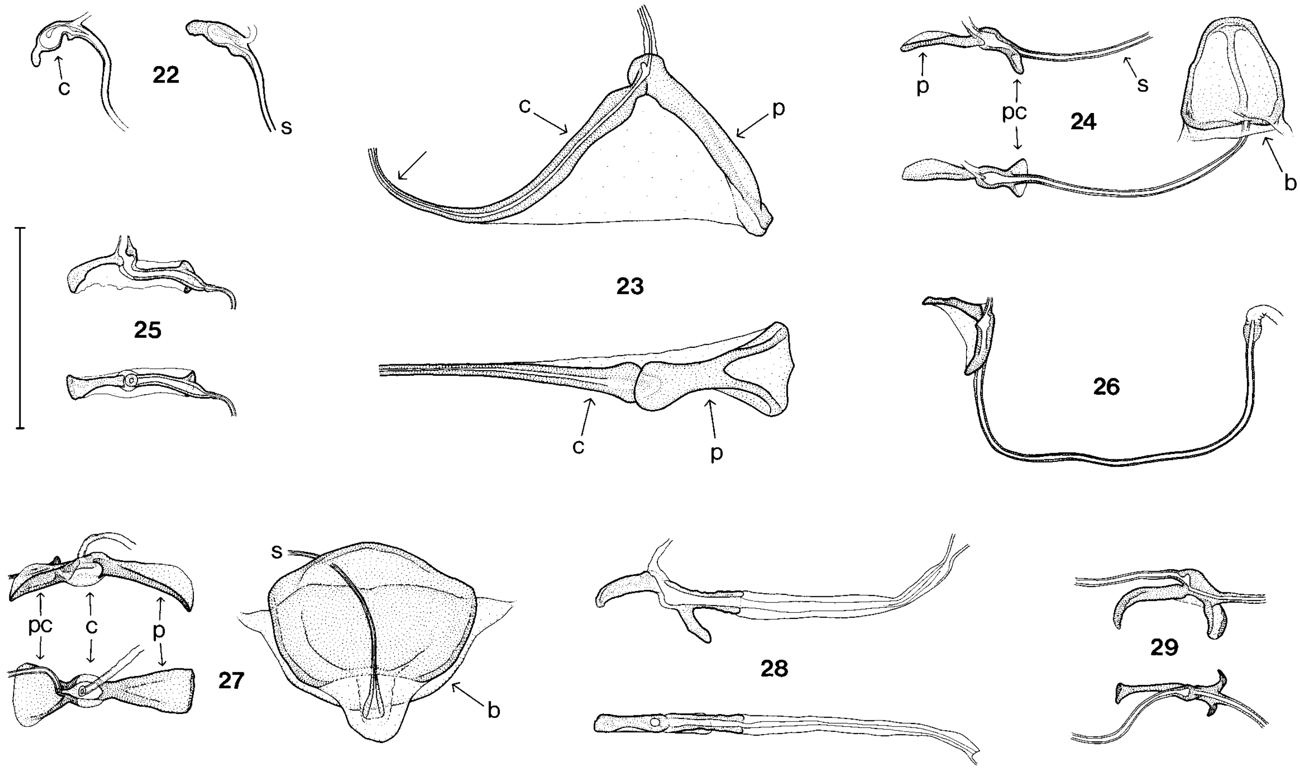
The dorsal lobe of the aedeagus of *Scopaeus* also provides phylogenetically informative features for both species and species groups. The aedeagus in *Luzea* and *Micranops* still has a short, lobiform dorsal lobe (char. 43:0) which is, however, derived in the former genus due to the remarkable inner setae (char. 44:1; Figs. 5, 6). Contrary to the aedeagus of *Hyperscopaeus*, which lacks a distinct dorsal lobe (char. 42:0; Figs. 7–9), those of the remaining *Scopaeus* are more or less elongate and strongly sclerotized (char. 43:2; Figs. 12, 15, 18, 21). Except for the simple ones of the *S. sericans* group or the *S. signifer* group (char. 45:1), other groupings within *Scopaeus* are characterized by a highly apomorphic dorsal lobe.

The phallobase of *Scopaeus* is divided by a strongly sclerotized, median ring (char. 72:1; Figs. 7–21) into a proximal and a more strongly sclerotized distal portion bearing lobes. Additional characters are provided by the structures beside the median foramen (chars 74, 75; Figs. 11, 17, 20).

Results

The cladistic analysis of the data matrix (Appendix 3; Electr. Suppl. 02–02, Pt 2) with NONA including 73 informative characters coded for West Palaearctic species of *Micranops* and *Scopaeus* resulted in a total of 1,195 most parsimonious cladograms (length 249 steps, CI = 82, RI = 95). The resulting bootstrap consensus tree (Fig. 40) shows that West Palaearctic taxa form several well-supported monophyletic clades, whereas their phylogenetic relationships remain unclarified. In most cases, the resulting clades agree with the informal species groups introduced by Frisch (1997–1999c), but are highly different from the subgenera described by Coiffait (1952, 1960, 1968, 1981, 1984).

Taking into account the geographical restriction of this analysis, the monophyly of the Scopaeina remains doubtful, because the New World genus *Orus* was not considered. However, all West Palaearctic taxa agree in



Figs. 22–29. Spermatheca (lateral and dorsal views) and spermathecal duct (not illustrated in full length) of 22) *Micranops pilicornis*; 23) *Hyperscopaeus* (*Scopaeus andrewesi*, India); 24) *S. laevigatus* group (*S. laevigatus*); 25) *S. minimus* group (*S. minimus*); 26) *S. longicollis* group (*S. kovaci*); 27) *S. elegans* group (*S. trifurcatus*); 28) *S. gracilis* group (*S. siculus*); 29) *S. debilis* group (*S. debilis*). Abbreviations: b = bursa copulatrix, c = chamber, p = process, pc = process of chamber, s = spermathecal duct . Scale = 0.1 mm.

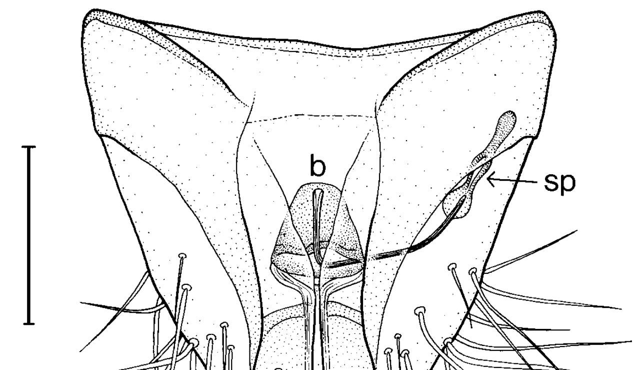
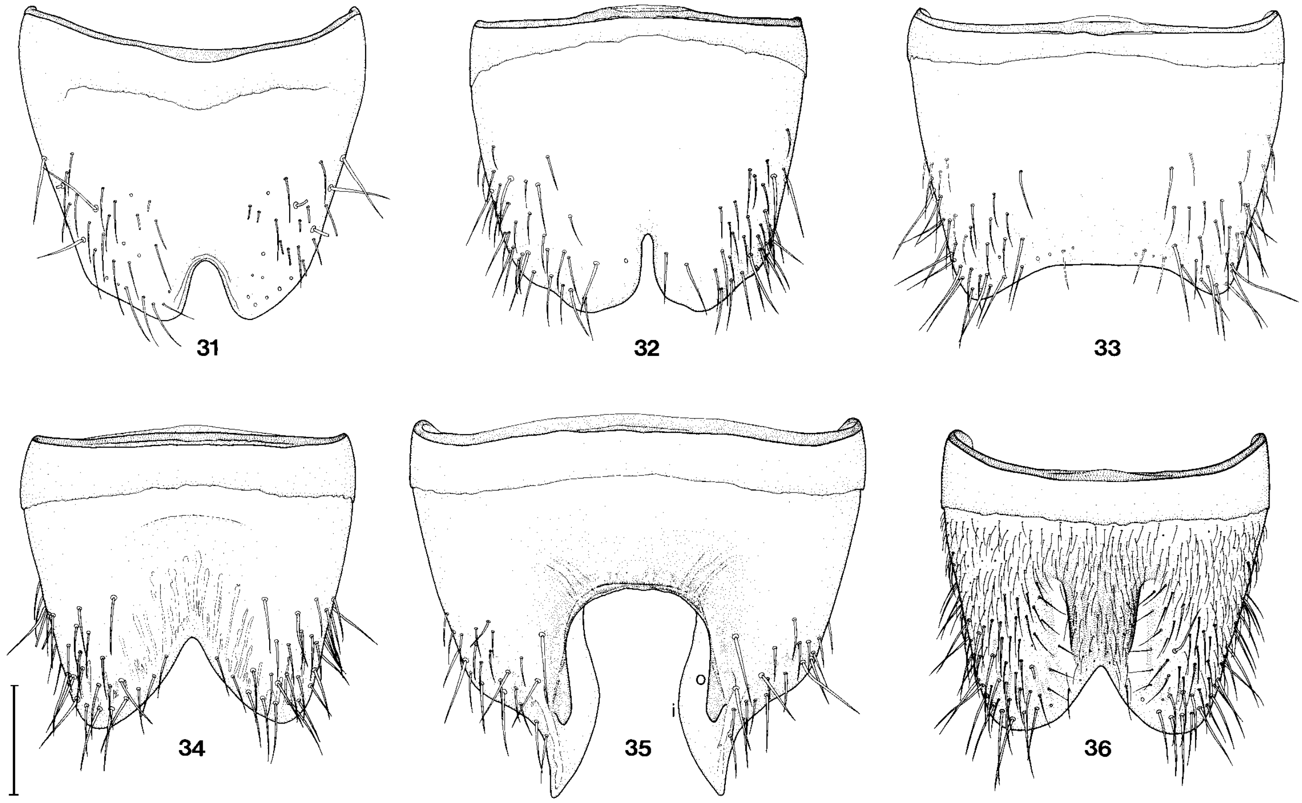


Fig. 30. *Scopaeus laevigatus* group: position of spermatheca and bursa copulatrix within genital segments of *S. laevigatus*, ventral view. Abbreviations: b = bursa copulatrix, sp = spermatheca. Scale = 0.1 mm.

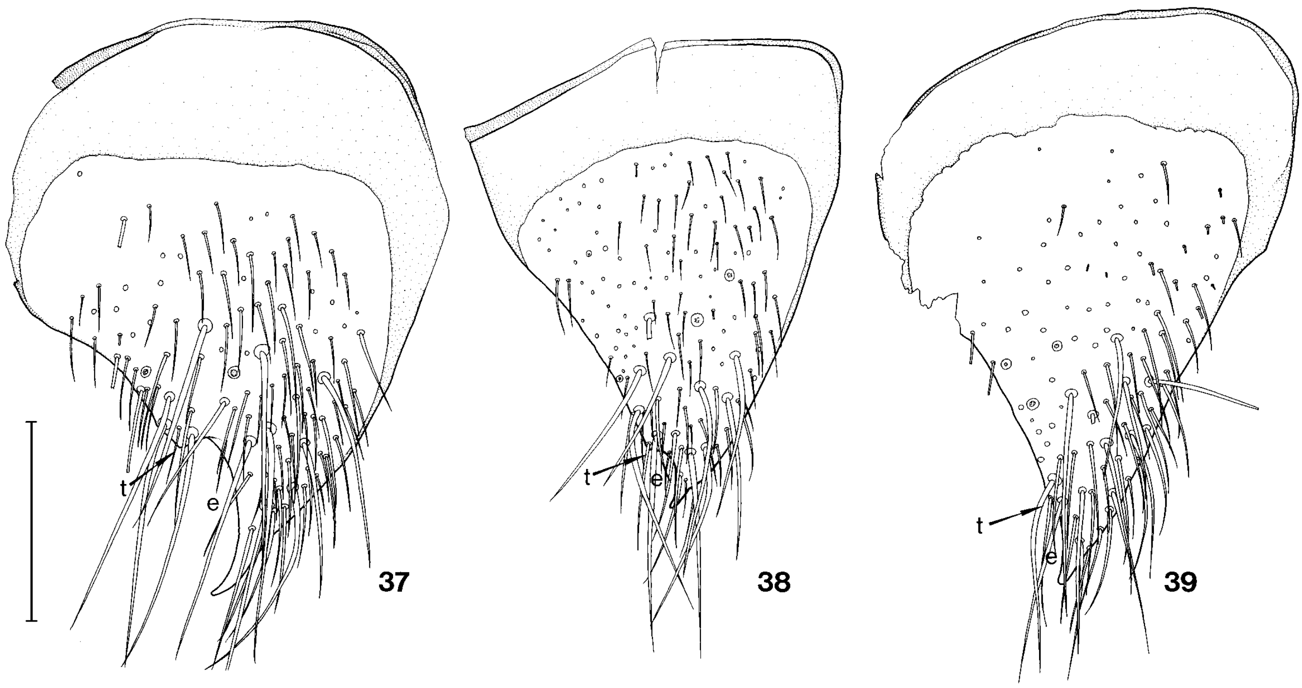
possessing a slender neck (char. 1:1), an oblong pronotum which is strongly tapering towards the narrow anterior margin (char. 2:2), a quadridentate labrum (char. 3:1), and an unidentate laterotergite 9 (char. 19:1). These characters are probably synapomorphies of Scopaeina.

The basal taxon of the Scopaeina is *Micranops*. The group is distinguished by a setiferous furrow behind the eyes (char. 4:1; Fig. 1b), thick median setae at the hind margin of the male abdominal sternite 7 (char. 21:1), and by the aedeagus (Figs. 4–6) with a stout flagellum without surrounding teeth (char. 28:2), a large, lobiform ventral endophallic process (char. 36:1) and a dorsal lobe bearing long inner setae (char. 44:1).

The next grouping represents *Scopaeus*. All species included share a two-piece spermatheca (char. 13:1; Figs. 23–29) and the sclerotized aedeagal ring between the phallobase and the remarkable distal lobes (char. 72:1; Figs. 7–21). Even though two-piece spermathecae occur in the scopaeine genera *Orus* and *Micranops* as well (Herman 1965a), *Scopaeus* is most likely monophyletic according to the aedeagal characters. Within *Scopaeus*, two highly different clades can be distinguished.



Figs. 31–36. Abdominal tergite 8 of male of 31) *Micranops* (*M. pilicornis*); 32) *Scopaeus debilis* group (*S. debilis*); 33) *S. gracilis* group (*S. gracilis*); 34) *S. elegans* group (*S. kurdistanicoides*); 35) *S. laevigatus* group (*S. biskrensis*); 36) *S. sulcicollis* group (*S. ponticus*). Scale = 0.1 mm. Abbreviations: i = inner border, o = outer border.



Figs. 37–39. Abdominal laterotergite 9 of 37) *Scopaeus laevigatus* group (*S. ebneri*); *S. minimus* group (*S. minimus*); *S. sulcicollis* group (*S. ponticus*). Scale = 0.1 mm. Abbreviations: e = dorsal emargination, t = dorsal tooth.

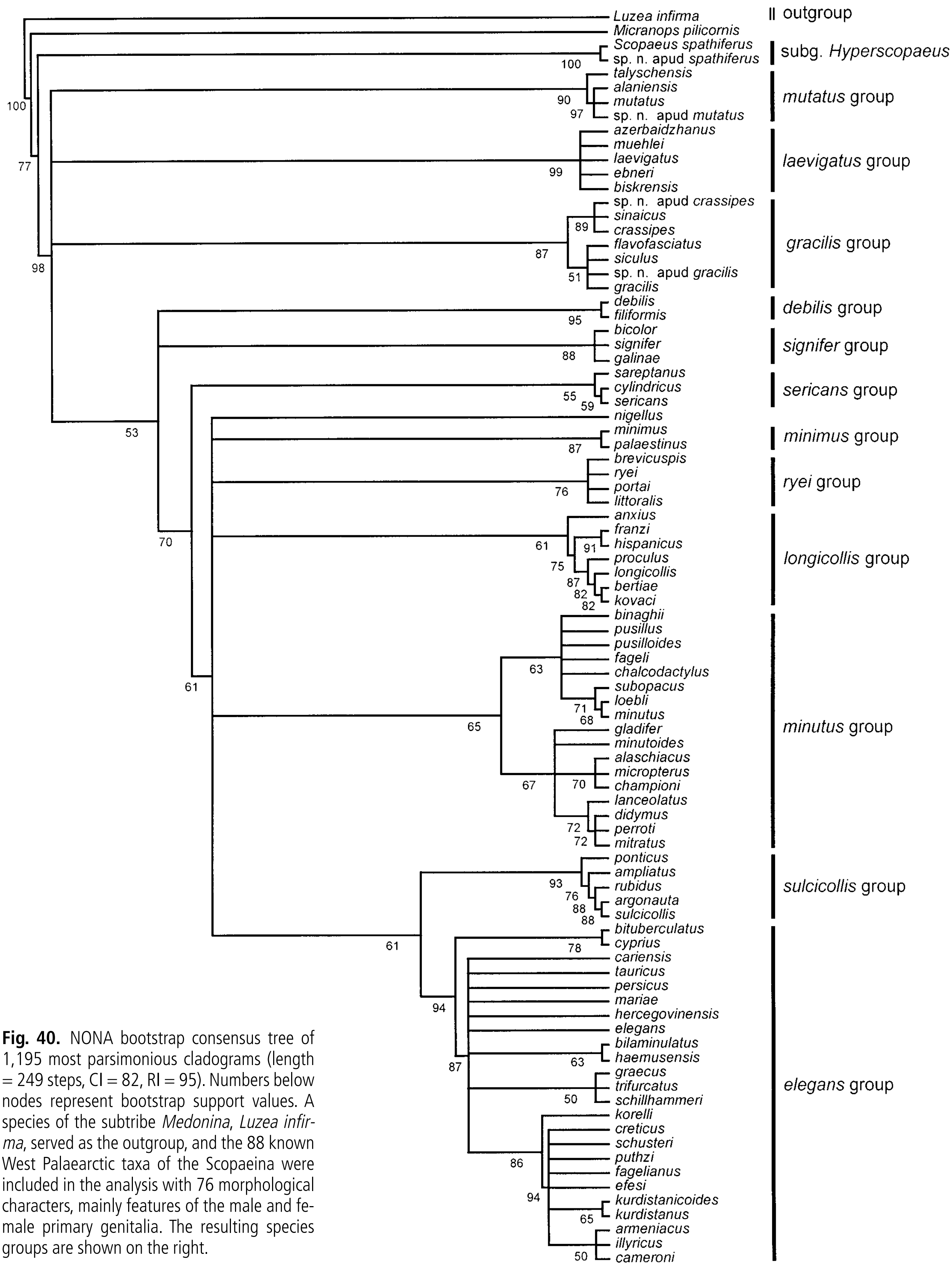


Fig. 40. NONA bootstrap consensus tree of 1,195 most parsimonious cladograms (length = 249 steps, CI = 82, RI = 95). Numbers below nodes represent bootstrap support values. A species of the subtribe *Medonina*, *Luzea infirma*, served as the outgroup, and the 88 known West Palaearctic taxa of the Scopaeina were included in the analysis with 76 morphological characters, mainly features of the male and female primary genitalia. The resulting species groups are shown on the right.

The first grouping, *Hyperscopaeus*, is distinguished by the following most likely derived characters: the extraordinarily slender neck is only one eighth of the width of the elongate, parallel head the hind margin of which is notably concave (chars 1:2, 6:0; Fig. 2). The lateral margins of the pronotum are parallel as well (char. 2:1). The extraordinarily wide protarsomeres are about three times as wide as long (char. 8:3). The females differ by the emarginate abdominal sternite 7 (char. 18:1), and sternite 8 of the males is more deeply emarginate than those of the remaining *Scopaeus*. *Hyperscopaeus* also differs in the notably larger aedeagus (Figs. 7–9) with a long, rather membranous, unipartite apical portion of the median lobe (chars 42:1, 57:1) with distinct lobes only at the very apex. This long, unipartite median lobe, however, corresponds to the primitive type of aedeagus of staphylinids (Blackwelder 1936, Naomi 1990) and is perhaps not an apomorphy. *Hyperscopaeus* is furthermore assumed as monophyletic due to the remarkably broad sclerotized ring of the phallobase (char. 73:9) and the derived position of the median foramen at the proximal end of the phallobase (char. 75:1). Despite the obviously apomorphic shapes of both the body and the aedeagus, *Hyperscopaeus* is linked with the outgroup according to the denticles or teeth (char. 27:0) along the flagellum (Figs. 7–9). Hence, this character has to be taken as plesiomorphic for Scopaeina. Judging from this large number of derived characters, *Hyperscopaeus* is considered to be a basal clade of *Scopaeus* and probably the sister group of the remaining *Scopaeus*.

The latter clade, here termed *Scopaeus* s. str., is proved as monophyletic according to the following synapomorphies: the chamber of the spermatheca is extended into a terminal process (char. 16:1; Figs. 24–29); the aedeagus (Figs. 10–21) bears well-developed distal lobes (char. 26:3) of which the dorsal lobe is strongly sclerotized and elongate (char. 43:2), and the remarkable apical lobes are testaceous and more or less enlarged ventrally (char. 58:2); the lengthened flagellum lacks the surrounding tooth-like structures (char. 28:3) of *Hyperscopaeus* (Figs. 7–9) and *Luzea*, and the phallobase bears lateral lobes (char. 76:2) with apical setae. However, both the lateral lobes and the apical setae are frequently strongly reduced (Figs. 13–15) or even lacking (Figs. 19–21).

Within *Scopaeus* s. str., the terminal species groups are predominantly well founded both by characters (Fig. 40) and geographically and therefore considered as monophyletic, whereas the results regarding the relationships among those species groups remain preliminary, bearing in mind the geographical restriction of this analysis.

The basal branch of *Scopaeus* s. str. comprises three well-founded groupings. The *S. mutatus* group is considered as monophyletic according to following features: the spermatheca is comparatively small with little-flexed portions, the process is dentate terminally (char. 17:7); the emargination of male sternite 8 is short, wide and almost semicircular (char. 25:1); the ventral process of the phallobase is very short and obtusely rounded (char. 34:3); the dorsal lobe has a separate distal portion which is evenly rounded at the apex and lacks ventral teeth (char. 46:2); the apical lobes have a distinct apical portion as well, are dorsally fused either completely (*S. talyschensis*) or except for the very apex (char. 61:1), and have parallel inner margins (char. 62:1); finally, the sclerotized ring of the phallobase is comparatively broad with rather slender lateral portions (char. 73:3). Judging from the characteristic shape of the flagellum (char. 29:5) and the distal portions of the apical lobes (chars 63:1, 64:1), the allopatric *S. alaniensis*, *S. mutatus* and an undescribed species from Central Turkey form a distinct clade, with *S. talyschensis* as the sister.

The *S. laevigatus* group (Frisch, in press) is postulated as monophyletic according to the following synapo-

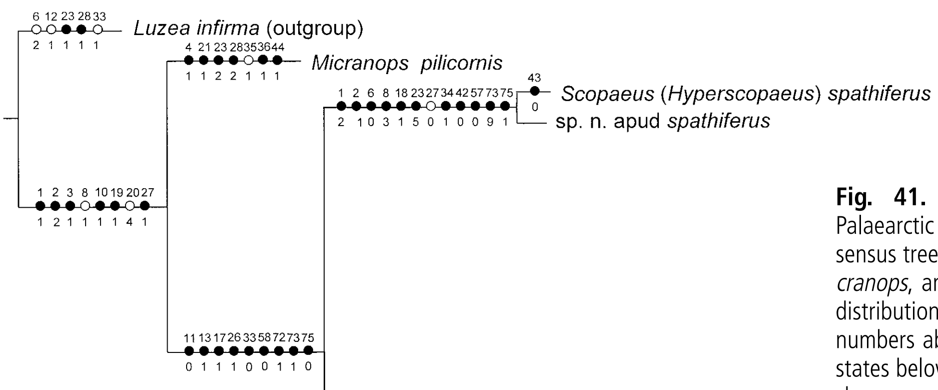


Fig. 41. Phylogenetic relationships of West Palaearctic Scopaeina; based on bootstrap consensus tree in Fig. 40, including the outgroup, *Micranops*, and *Hyperscopaeus*. The character state distribution is shown on each node, with character numbers above each circle symbol, and character states below. Non-homoplasious forward changes shown as solid circles, homoplasious changes as open circles.

morphies: the short spermathecal duct ends in a remarkable, strongly sclerotized bursa (char. 14:2; Figs. 24, 30); the dorsal emargination of laterotergite 9 is larger than in other *Scopaeus* and marked by a strong tooth (char. 20:1; Fig. 37); the distal emargination of the male sternite 8, which is, however, simplified secondarily in *S. muehlei* (char. 23:4), is very deep and surrounded by a strongly sclerotized outer margin which is drawn out into two distal teeth (char. 23:3; Fig. 35); the apical lobes of the aedeagus have enlarged distal portions (char. 61:2) which are triangular and distinctly set off against the basal portions in ventral view (char. 62:2); the lateral portions of the sclerotized ring of the phallobase are, in dorsal view, transverse and widely separate (char. 73:4). The *S. laevigatus* group splits into subgroups, of which only the *S. laevigatus* subgroup occurs in the West Palaearctic (Frisch, in press). Characteristics of the latter are the lamelliform ventral process of the phallobase (char. 34:4) and the shape of the distal portion of the dorsal lobe, which is emarginate at the apex and bearing two pairs of ventral teeth and two ventral lamellae.

The next clade, here named the *S. gracilis* group, comprises the *S. gracilis* group sensu Frisch (1998) and three West Palaearctic species which share the characters of the African *S. crassipes* and *S. peregrinus* groups as established by Fagel (1973). The *S. gracilis* group as here defined is considered to be monophyletic due to following features: distal emargination of male sternite 8 (Fig. 33) short, wide (char. 23:6) and with a convex middle (char. 25:2); both the apical lobes (char. 49:5) and the dorsal lobe (char. 45:5) of the aedeagus (Figs. 13–15) are asymmetrical, as is the remarkably lengthened flagellum which is at least as long as the apical lobes (char. 29:2); the lateral portions of the very broad ring of the phallobase, in dorsal view (Fig. 15), are large but separate (char. 73:5). Two subgroups are distinguished. The *S. crassipes* subgroup is different due to the conspicuously short portions of the spermatheca (char. 17:6) and the shape of the spermathecal duct which, without thickening, becomes hyaline (char. 14:5). The aedeagus is characterized by a variable ventral process of the phallobase (char. 34:5), lateral lobes of unequal length with long setae (char. 39:8), and by comparatively stout, very asymmetric apical lobes (char. 69:2). Bearing in mind the large number of African and Oriental species, the *S. crassipes* subgroup, however, is paraphyletic. Unlike this, the *S. gracilis* subgroup is monophyletic according to a lateral tooth at the base of the flagellum (char. 32:2; Fig. 14), the absence of lateral lobes (char. 39:7), and the apical lobes being extraordinarily slender (char. 69:1; Figs. 13–15).

The next clade within *Scopaeus* s. str. is poorly supported and lacks obvious synapomorphies. However, it separates two well–defined monophyletic groups, the *S. debilis* group, established by Frisch (1999), and the *S. signifer* group (Frisch 1997c).

The *S. debilis* group is considered to be monophyletic according to the strong, shortly tapering flagellum of the aedeagus (char. 29:9; Fig. 10) and the small, additional canal of the chamber of the spermatheca (char. 17:5; Fig. 29). Two subgroups are distinguished, of which only the *S. debilis* subgroup (= *S. tenuis* group sensu Fagel 1973) is known from the West Palaearctic (Frisch 1999). Derived characters of the latter are the very narrow emargination of the male sternite 8 (char. 23:7; Fig. 32), the hook-shaped ventral endophallic processes (char. 36:9; Fig. 10), the strongly reduced lateral lobes with few ventrally pointing setae (char. 39:6; Figs. 10, 11), and the vestigial dorsal lobes (45:8; Fig. 12).

The *S. signifer* group (Frisch 1997c) is characterized by the following synapomorphies: the spermatheca is stout with strongly flexed portions and a right-angled, upflexed spermathecal duct (char. 17:2); the hind margin of male sternite 7 has a deep, rectangular emargination (char. 21:2), and the terminal sclerites are sparsely setose (char. 22:1). Sternites 8 of the males agree in short, distal emarginations with wave-like, convex lateral margins (char. 23:8); the strong flagellum of the aedeagus shortly tapers at the apex and reaches the apices of the apical lobes (char. 29:8), and the obtuse lateral lobes bear a line of setae which are flexed ventrally and therefore invisible in dorsal view (char. 39:9).

Whereas the preceding taxa within *Scopaeus* share more or less elongate distal antennomeres, the next clade

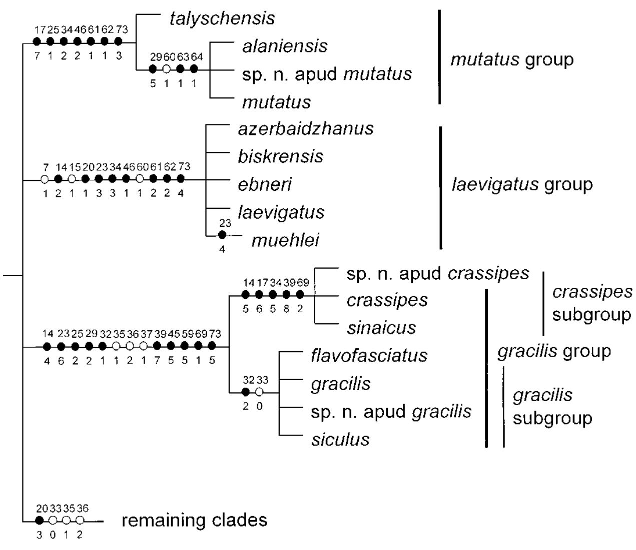


Fig. 42. Phylogenetic relationships of West Palaearctic Scopaeina; part of bootstrap consensus tree in Fig. 40, including the basal species groups of *Scopaeus* s. str. (*S. mutatus*-, *S. laevigatus*-, and *S. gracilis* groups). The character state distribution is shown on each node, with character numbers above each circle symbol, and character states below. Non-homoplasious forward changes shown as solid circles, homoplasious changes as open circles.

comprises species groups with square or somewhat transverse distal portions (char. 11:2). This character, however, occurs in many staphylinids, as well as in *Luzea* and *Micranops*. The following species of *Scopaeus* agree also in a simple, triangular emargination of the male sternite 8 (char. 24:1; as in Fig. 34), but lack definite synapomorphies.

The *S. sericans* group is probably monophyletic according to the ventrally curved flagellum (char. 29:4), the remarkable, hook-shaped ventral endophallic process (char. 36:6), and the broad sclerotized ring of the phallobase, the lateral portions of which are very close in dorsal view (char. 73:6). Within this grouping, *S. cylindricus* and *S. sericans* are linked by the apical lobes of the aedeagus being studded with long setae (char. 67:1), and by the small, strongly sclerotized bursa of the spermathecal duct (char. 15:2).

The next clade again lacks synapomorphies. It comprises the following species groups, whose phylogenetic relationships remain doubtful. First it separates *S. nigellus*, which cannot be assigned to one of the following clades because the male is unknown.

The *S. minimus* group was already established by Frisch (1998). It is identified as monophyletic according to the notably lengthened chamber of the spermatheca (char. 17:4; Fig. 25), outreaching lateral lobes with very long setae (char. 40:5), the deeply emarginate dorsal lobe with apical teeth strongly recurved towards the phallobase (char. 45:9), and the characteristic shaping of the apical lobes (char. 59:8).

The *S. ryei* group (Frisch 1998) is considered as monophyletic based on the following diagnostic features: the ventral endophallic process of the aedeagus is curved and emarginate at the apex (char. 36:7), the long setae of the apical lobes are pointing ventrally (char. 40:4), and the apical lobes are strongly reduced and much shorter than the strongly enlarged, bilobed dorsal lobe (chars 45:4, 59:6).

The *S. longicollis* group comprises *S. anxius*, the *S. longicollis* group sensu Frisch (1999c), and the *S. hispanicus* group (Frisch 1997c), which all agree in the shape of the head (char. 6:3) and particularly in large, strongly projecting lateral lobes which are ventrally studded with numerous setules (char. 39:4). The *S. hispanicus* and *S. longicollis* subgroups agree in the following synapomorphies: the spermathecal duct is rather short, its sclerotized section shows a distinct terminal thickening (char. 14:3; Fig. 26), and sternite 8 of the females carries a densely setose median ridge with neighbouring, little-setose planations (char. 24:5; similar to Fig. 36). Hence, these two taxa are taken as sister groups. The *S. hispanicus* subgroup is monophyletic according to the long, hook-shaped, apically emarginate ventral endophallic process of the aedeagus (char. 36:8), the prominent lateral lobes, which became membranous and lost the setules (char. 39:5), and apical lobes with distinct, membranous apical portions (char. 59:9). The *S. longicollis* subgroup is considered as monophyletic according to the dorsal lobe, which bears two distal and two ventral teeth (char. 47:1). The distal teeth are widely separated (char. 48:1) in *S. bertiae*, *S. kovaci* and *S. longicollis*, which probably represent a monophyletic group with *S. proculus* as its sister. Moreover, *S. bertiae* and *S. kovaci* are taken as sister species according to the moderately developed lateral lobes.

The *S. minutus* group is considered to be monophyletic according to the ventral denticles of the flagellum (char. 29:0) and the knife-shaped apical lobes (Figs. 16–18) which, in most species, are emarginate ventrally (char. 59:2). It comprises two monophyletic sister groups, the *S. minutus* and *S. micropterus* subgroups. The former, which includes the *S. minutus* and the *S. pusillus* groups sensu Frisch (1997c), is different according to the short, triangular dorsal lobe (char. 50:1, 50:2), whereas the *S. micropterus* subgroup is characterized by short lateral lobes with long apical setae (char. 40:7; Figs. 16–18) and a very long and slender, deeply emarginate dorsal lobe (char. 49:2; Fig. 18). Within the *S. minutus* subgroup, *S. loebli*, *S. minutus* and *S. subopacus* form a monophyletic group according to the short setae of the apical lobes (char. 40:6), the stout apical teeth of the dorsal lobe (char.

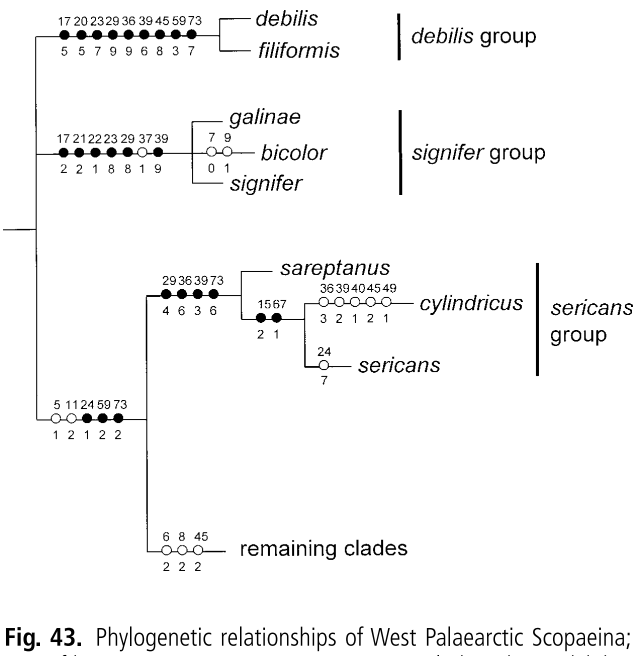


Fig. 43. Phylogenetic relationships of West Palaearctic Scopaeina; part of bootstrap consensus tree in Fig. 40, including the *S. debilis*-, *S. signifer*-, and *S. sericans* groups. The character state distribution is shown on each node, with character numbers above each circle symbol, and character states below. Non-homoplasious forward changes shown as solid circles, homoplasious changes as open circles.

50:2), and the deeply emarginate apical lobes with straight, slender distal halves (chars 65:4, 66:3). Moreover, *S. loebli* and *S. minutus* are probably sister species according to the widely separate distal teeth of the short, triangular dorsal lobe (char. 51:2). Even though shown as a polytomy in the bootstrap consensus tree (Fig. 40), *S. chalcodactylus*, *S. pusillus* and *S. pusilloides* form a monophyletic group as well according to the characteristic apical lobes, the apices of which are strongly flexed dorsally (char. 65:3). *Scopaeus binaghii* and *S. fageli* are obviously close to this grouping. The *S. micropterus* subgroup first comprises *S. minutoides* and *S. gladifer*, which agree in the long, deeply emarginate dorsal lobes with adjacent apical teeth (char. 52:2). In *S. alaschiacus*, *S. championi* and *S. micropterus*, those teeth are strongly diverging (char. 52:3; Fig. 18) and bearing apical teeth or denticles (char. 53:1). The species allied to *S. didymus* are characterized by the male sternite 8 with a distinct median ridge and lateral, asetose planations (char. 24:4), and by features of the aedeagus such as the hook-shaped ventral endophallic process (char. 36:4), long, slender lateral lobes (char. 40:2), and apical lobes with a shallow, ventral emargination and a dorsally curved apex (65:1). Judging from the slender dorsal lobe, which is emarginate at the distal half only (char. 52:1), and from the deep emarginations of the apical lobes (char. 65:2), *S. didymus*, *S. mitratus* and *S. perroti* constitute a monophyletic subgroup.

The next clade is made up of the *S. sulcicollis* group, which was defined and revised by Frisch (1997c, 1999b), and the *S. elegans* group (e.g. Frisch 1994, Frisch & Wolters 1999). Both taxa form a monophyletic group according to the lack of lateral lobes, which are, however, indicated by few setules (char. 76:1; Figs. 19, 20); the dorsal lobe with various ventral teeth (char. 45:3); but in particular according to an inner row of setae of the apical lobes (char. 59:4), which, within the *S. elegans* group, occurs in the basal *S. cyprius* subgroup only.

The *S. sulcicollis* group is well founded according to the small and feebly sclerotized bursa of the spermathecal duct (char. 15:3) and the asymmetric apical lobes of the aedeagus, which bear an inner row of setae (chars 68:1, 68:2). Within this monophyletic group, the male sternites 8 of *S. rubidus*, *S. argonauta* and *S. sulcicollis* agree in having a median ridge (as in Fig. 36) which is strongly setose at the distal margin and laterally marked by setose planations (char. 24:6). *Scopaeus argonauta* and *S. sulcicollis* are probably sister species according to the short dorsal lobe which bears two short, ventrally curved apical teeth (char. 54:1).

The *S. elegans* group is considered as monophyletic according to the extremely lengthened, strongly winding

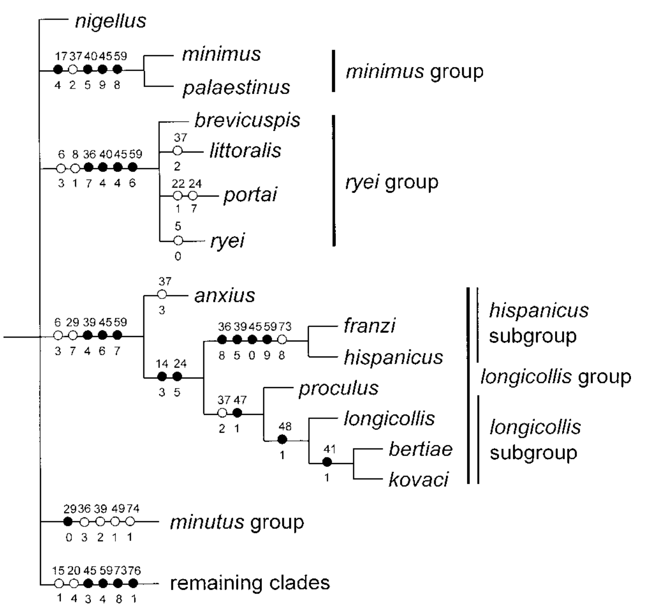


Fig. 44. Phylogenetic relationships of West Palaearctic Scopaeina; part of bootstrap consensus tree in Fig. 40, including the *S. minimus-*, *S. ryei-*, and *S. longicollis* groups. The character state distribution is shown on each node, with character numbers above each circle symbol, and character states below. Non-homoplasious forward changes shown as solid circles, homoplasious changes as open circles.

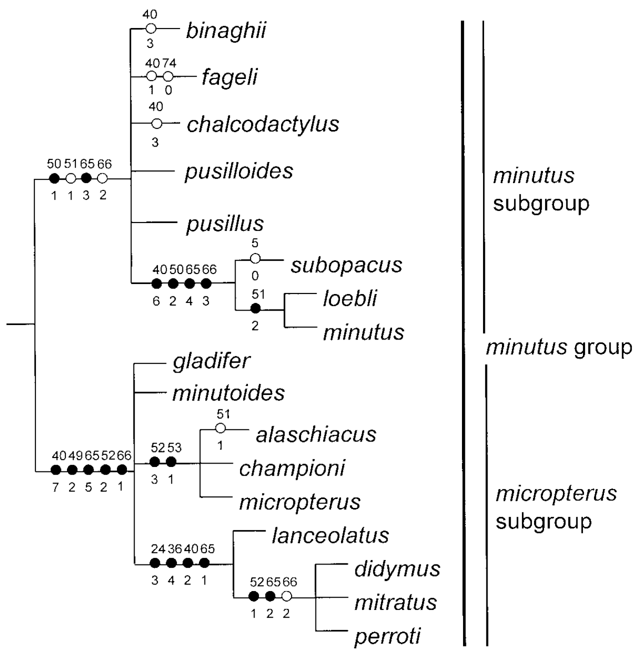


Fig. 45. Phylogenetic relationships of West Palaearctic Scopaeina; part of bootstrap consensus tree in Fig. 40, treating the *S. minutus* group. The character state distribution is shown on each node, with character numbers above each circle symbol, and character states below. Non-homoplasious forward changes shown as solid circles, homoplasious changes as open circles.

spermathecal duct which ends in a large, strongly sclerotized, species-specific bursa (char. 14:1; Fig. 27); the deep emargination in at least the hind third of the male sternite 8 (char. 24:2; Fig. 34); and the flagelliform ventral endophallic process of the aedeagus (char. 36:5; Figs. 19, 20). The most basal grouping within the *S. elegans* group, the *S. cyprius* subgroup, comprises *S. cyprius* and *S. bituberculatus*, which share the inner row of setae of the apical lobes (char. 59:4) and a strongly lengthened, acute dorsal lobe (char. 54:4). The other species are characterized by a comparatively large spermatheca with little-flexed portions (char. 17:3; Fig. 27), and by a flagellum with apical teeth (char. 29:6; Fig. 20). Within the polytomous *S. elegans* group, the *S. armeniacus* subgroup as defined by Frisch (1994) and Frisch & Wolters (1999) is well founded, even though *S. elegans* has to be excluded. Unlike this, the *S. bilaminulatus* subgroup (Frisch 1994) was not supported by this analysis, because its diagnostic character, the little emarginate, various ventral teeth bearing dorsal lobes (char. 54:2), proved to

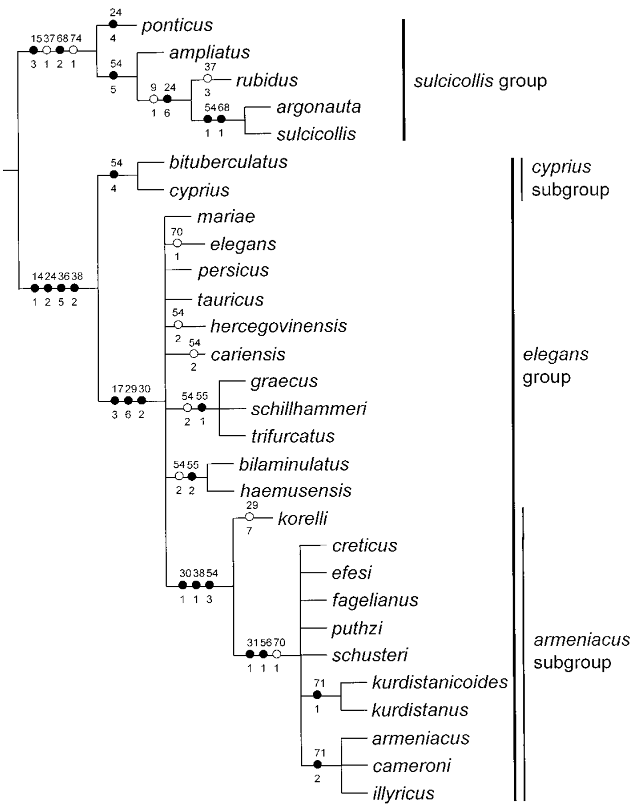


Fig. 46. Phylogenetic relationships of West Palaearctic Scopaeina; final section of bootstrap consensus tree in Fig. 40, including the *S. sulcicollis*- and *S. elegans* groups. The character state distribution is shown on each node, with character numbers above each circle symbol, and character states below. Non-homoplasious forward changes shown as solid circles, homoplasious changes as open circles.

be a symplesiomorphy. However, *Scopaeus bilaminulatus* and *S. haemusensis* are sister species according to the bidentate dorsal lobe (char. 55:2), and *S. graecus*, *S. trifurcatus* and *S. schillhammeri* agree in dorsal lobes with three remarkable ventral teeth (char. 55:1).

Apart from the deeply emarginate dorsal lobe, which is extended into two ventrally curved teeth of unequal length (char. 54:3; Figs. 19–21), the *S. armeniacus* subgroup is characterized by the long, S-shaped flagellum (Fig. 19) which is orientated longitudinally (char. 30:1), and by the flagelliform ventral endophallic process (Figs. 19, 20) the apex of which is flexed to the right in ventral view (char. 38:1). Except for the basal *S. korelli*, the remaining species of this subgroup agree in the strongly lengthened, S-shaped flagellum which is as long as the dorsal lobe (char. 31:1), and particularly in the lobiform apical teeth of the dorsal lobe (char. 56:1). Amongst those species, *S. kurdistanus* and *S. kurdistanicoides* are sister species according to the slender apical lobes with a very shallow disto-ventral emargination (char. 71:1; Fig. 19). Likewise, *S. armeniacus*, *S. cameroni* and *S. illyricus* form a monophyletic group judging from the strongly hook-shaped apex of the apical lobes (char. 71:2).

Biogeography

A proper biogeographical analysis with West Palaearctic *Scopaeus* is premature at the present state of knowledge. Despite the relatively restricted geographical distributions of most species, the taxon cladogram is not sufficiently resolved from a biogeographical point of view. On a much coarser level, e.g. that of widely distributed species groups, the cladogram lacks the non-Palaearctic members. Much information on distribution patterns of West Palaearctic *Scopaeus* and *Micranops* has been published by Frisch (1994–2001) and Frisch & Wolters (1999), and basic distributional information is compiled in the species catalogue (Appendix 2; Electr. Suppl. 02–02, Pt 1). The biogeography of the species groups confirmed by the present cladistic analysis is briefly discussed below.

A large number of species and most species groups of West Palaearctic *Scopaeus* without doubt originate in the Mediterranean region. Except for the Afroeremial regions of North Africa, Saudi Arabia or Iraq, the species richness of *Scopaeus* remarkably increases towards the south, and only eleven species occur north of the Alps. Besides Mediterranean and Near Eastern faunal elements, some West Palaearctic Scopaeina such as *Micranops* and *Hyperscopaeus*, which are species-rich in the Palaeotropical realms (sensu Müller 1981), originate in different zoogeographical regions. Likewise, the *S. debilis* and *S. laevigatus* groups are very widespread and occur in the West Palaearctic with few species only.

Micranops is distributed world-wide and rather speciose in the Old World. Twelve species are described from the Afrotropical region (Fagel 1973), and several unnamed ones occur in the Oriental region. *Micranops pilicornis*, the only species in the West Palaearctic, shows a Pontomediterranean and Caspian (Gusarov 1992b) type of distribution. It was recently found in southern Italy (Abruzzese Mts., Campania) and hence has a trans-adriatic distribution as described for many organisms (e.g. Gridelli 1950, Witte 1965).

Hyperscopaeus is very speciose in the Palaeotropical realm. Both West Palaearctic members are restricted to the Nile Valley and obviously Afrotropical faunal elements.

The *S. mutatus* group, distributed in the Near East, comprises *S. talyschensis* from the southern Caspian region and the Anatolian species *S. alaniensis* and *S. mutatus* as well as an undescribed one, which constitute a monophyletic group of allopatric species.

The *S. laevigatus* group comprises 20 known species in the Palaearctic and Oriental regions, of which one also occurs in the Afrotropical region (Frisch, in press). Five species of the Palaearctic *S. laevigatus* subgroup are known from the West Palaearctic. Whereas *S. laevigatus* is widely distributed from West Europe to the far east of Siberia and China, the remaining species have notably smaller ranges in the Mediterranean and Caspian regions (Frisch, in press).

The *S. gracilis* group is distributed throughout the Old World. *Scopaeus crassipes*, *S. sinaicus* and an undescribed species from the Canaries, which reach the eremial regions in the very south of the West Palaearctic, belong to the species-rich Palaeotropical *S. crassipes* subgroup. The *S. gracilis* subgroup is distributed in the Palaeotropics as well. In the West Palaearctic, it comprises the allopatric species *S. gracilis*, widespread in mountainous regions of the southern and temperate West Palaearctic, *S. flavofasciatus* from Cyprus, *S. siculus* from South Italy, and an undescribed Sardinian species.

The *S. debilis* group comprises five species in the tropics and warm-temperate regions of the Old World. Whereas the *S. mendosus* subgroup is Afrotropical only, two species of the *S. debilis* subgroup (= *S. tenuis* group sensu Fagel 1973) are known from the West Palaearctic (Frisch 1999): *Scopaeus debilis* is Holomediterranean, whereas *S. filiformis*, widely distributed in the Palaeotropical realm, reaches the Palaearctic only in the very south (Algeria, Egypt, Iran, Morocco, Saudi Arabia, Turkey).

The *S. signifer* group (Frisch 1997c) comprises three allopatric species which are distributed thoughout the southern West Palaearctic to Tadzhikistan in the east.

The *S. sericans* group is known from the West Palaearctic only. It comprises *S. cylindricus* from South France, *S. sericans*, distributed in mountainous regions of southern Central Europe (Alps, Carpathians), and *S. sareptanus* from South Russia.

The *S. minimus* group (Frisch 1998) only comprises *S. minimus*, widespread in Central and South-East Europe and Anatolia, and the Near Eastern *S. palaestinus*.

The *S. ryei* group (Frisch 1998) comprises four species in the West Mediterranean, of which only *S. ryei* is distributed thoughout large parts of Central Europe and the northern Balkans.

The West Mediterranean *S. longicollis* group is made up of *S. anxius* from South France and the Iberian Peninsula, the *S. longicollis* group sensu Frisch (1999c) from South-West Europe and North Africa, and the *S. hispanicus* group sensu Frisch (1997a). Whereas the latter grouping consists of two allopatric Iberian species, the former comprises the North African *S. bertiae* and *S. proculus*, the distribution of which is poorly known, *S. kovaci* from Morocco and South Spain, and the widespread *S. longicollis* which occurs northwards to Central France and western Germany (Frisch 1996).

The *S. minutus* group, species-rich in the West Palaearctic region, is widespread in the Holarctic. *Scopaeus pusillus* is known to range east to Central Asia (Altai Mts.), and *S. minutus* was recorded from Canada (Montréal). The terminal monophyla of the *S. minutus* group are made up of allopatric taxa. *Scopaeus loebli* (Anatolia), *S. minutus* (Canada, Europe) and *S. subopacus* (Madeira), for instance, constitute a monophyletic group of allopatric species just as do *S. chalcodactylus* from the Caucasus and East Anatolia, the widespread Palaearctic *S. pusillus* and the Iberian *S. pusilloides*. The North African *S. binaghii* and *S. fageli* are closely related to the latter grouping. The *S. micropterus* subgroup comprises allopatric species, too, such as *S. minutoides* from West Anatolia and *S. gladifer*, distributed around the Black Sea and in South Russia (Samara), or *S. alaschiacus* from Cyprus, *S. championi* from the Alps, Carpathians and the Balkans, and *S. micropterus* from northern Italy. Likewise, *S. didymus* (Iberian Peninsula, South France, Tyrrhenian Islands), *S. mitratus* (Italy, Corfu) and *S. perroti* (North Africa) constitute a monophyletic group of allopatric taxa as well.

The *S. sulcicollis* group is distributed in the West Palaearctic but unknown from North Africa (Frisch 1999b). It comprises five species, amongst which *S. sulcicollis*, widespread in South and Central Europe, and the Caucasian *S. argonauta* are obviously allopatric sister species.

The species-rich *S. elegans* group is widespread in the Pontomediterranean region and the Near East (Frisch, in press). It also consists mainly of groups of allopatric species. The basal *S. cyprius* subgroup comprises the allopatric species *S. cyprius* from Cyprus and *S. bituberculatus* from southern Anatolia. *Scopaeus bilaminulatus* from eastern Anatolia and *S. haemusensis* from Bulgaria and Northwest Anatolia are allopatric sister species, as are *S. graecus* from the South Balkans, *S. trifurcatus* from South Anatolia and *S. schillhammeri* from eastern Anatolia and Iran. Likewise, the monophyletic *S. armeniacus* subgroup comprises ten allopatric species from Albania eastward to Armenia and North Iran (Frisch, in press).

Conclusions

Character evolution

This phylogenetic study, even though restricted to the West Palaearctic, makes some assumptions concerning general tendencies in the evolutionary process both towards and within *Scopaeus*. As most underlying structures, predominantly features of the aedeagus and the spermatheca, occur in groupings of *Scopaeus* from the remaining zoogeographic realms as well, the following evolutionary hypotheses are probably representative for the whole group.

In *Scopaeus*, characters of the body depend rather more on habits and niche choice than on relations. Nevertheless, whereas most basal *Scopaeus* (*S. mutatu*s - *S. longicollis* groups) share large eyes, long elytra and functional hind wings and have comparatively large geographical ranges, more strongly derived species agree in smaller eyes, and many of them are wing-dimorphous or flightless and, hence, distributed in small ranges. Therefore we assume an evolutionary tendency within *Scopaeus* towards the loss of ability to fly and endemism.

Bearing in mind the wide neck of most staphylinids and paederines, the comparatively slender neck of the Scopaeina (Figs. 1–3) has to be regarded as derived. This character, however, is found both in many staphylinids and paederines and most likely evolved several times.

During evolution, the genital segments of staphylinids became variously modified (Blackwelder 1936, Uhlig 1989). The unidentate laterotergite 9 of the Scopaeina (Figs. 37–39) is here regarded as apomorphic because in many staphylinids, just as in the outgroup *Luzea*, these sclerites have two apical teeth of the same length. Unlike this, the simple, triangular emargination of the distal margin of male sternite 8 of many *Scopaeus* (Fig. 34) is found in most staphylinids, and thus primitive. However, this emargination is highly derived and apomorphic for various groupings of *Scopaeus* such as the *S. laevigatus*- (Fig. 35) or the *S. mutatus* group.

The two-piece spermatheca (Figs. 23–29), probably a sperm-pump, is an important synapomorphy connecting *Scopaeus*, *Micranops* and the New World genus *Orus*. However, the additional joint of the spermatheca is absent in the West Palaearctic *Micranops pilicornis* (Fig. 22) as well as in both the outgroup and the remaining staphylinids. Perhaps it was reduced secondarily in *M. pilicornis*. Within *Scopaeus*, however, the spermatheca of *Hyperscopaeus* (Fig. 23) lacks the typical process of the chamber, an important apomorphy of *Scopaeus* s. str. (Figs. 24–29). This process is an apophysis for muscles as well (sperm-pump). The characteristic bursa (Figs. 24, 27, 30) at the end of the spermathecal duct of some species groups is considered to be an apomorphy of *Scopaeus*, too. Because it occurs in some unrelated groupings (e.g. the *S. laevigatus* and *S. elegans* groups) only, it might have been reduced several times. Even though variously sclerotized bursal sacs are known in Coleoptera (e.g. Heberdey 1931), they have not been described from other staphylinids yet.

Regarding the various derived character states of the aedeagus of both Paederinae and Scopaeina, it is difficult to recognize evolutionary tendencies. According to Naomi (1990), the apical part of the median lobe is reduced or even lost in many paederines. Thus, bearing in mind the short aedeagal lobes of *Luzea* and the basal scopaeine taxa *Micranops* (Figs. 4–6) and *Orus*, the distal lobes of the aedeagus of *Scopaeus* (Figs. 7–21) probably became enlarged, more prominent and specific to species and species groups. However, it remains doubtful whether the long, membranous apical portion of the median lobe in *Hyperscopaeus* (Figs. 7–9) corresponds to the unipartite median lobe as described by, e.g., Blackwelder (1936) for the primitive aedeagus of staphylinids, or whether it must be taken as a secondary fusion of distinct distal lobes. The presence of short, distinct apical lobes near the apex of the median lobe, however, indicates a secondary fusion of distinct lobes.

Hyperscopaeus, *Micranops* and the outgroup Luzea lack the setiferous, so-called lateral lobes of *Scopaeus* s. str. (e.g. Figs. 16–18), which are thus considered to be an apomorphy of *Scopaeus* s. str. These lateral lobes, which are not parameres but part of the median lobe (Herman, pers. comm), reveal an obvious tendency of reduction (e.g. Figs. 13–15), and strongly derived clades such as the *S. sulcicollis* and *S. elegans* groups even share completely reduced lateral lobes which are indicated by very few setules only (Figs. 19–21).

The aedeagus of *Scopaeus* reveals a tendency to lengthening of the flagellum. Whereas it is rather short and stout in *Luzea* and *Micranops* (Figs. 4–6), it is slender in *Scopaeus* and frequently strongly extended in groupings – which are, however, little related – like the *S. gracilis* (Figs. 13–15) and the *S. minimus* groups or the *S. armeniacus* subgroup (Figs. 19–21) within the *S. elegans* group.

Within *Scopaeus*, the phallobase of basal groups such as *Hyperscopaeus*, the *S. mutatus* and *S. laevigatus* groups or the *S. crassipes* subgroup of the *S. gracilis* group have a ventral process (char. 34; Figs. 7, 8). It is absent in both the outgroup and *Micranops* and probably an apomorphy of *Scopaeus*, which, however, became lost in more derived taxa. Unlike this, except for the basal *S. mutatus* and S. *laevigatus* groups, West Palaearctic species of *Scopaeus* s. str. share a ventral process of the endophallic structures (char. 35:1; Figs. 10–21), which is lacking in both the outgroup and *Hyperscopaeus*. The large, ventral lobe of the aedeagus of *Micranops* (Figs. 4, 5) is perhaps homologous. In this case the endophallic process would be a synapomorphy for *Micranops* and *Scopaeus*, which, however, was reduced in *Hyperscopaeus* and the *S. mutatus* and *S. laevigatus* groups.

Generalizing evolutionary tendencies within West Palaearctic Scopaeina, it turned out that the aedeagus developed various highly derived structures of the distal lobes and the endophallus, which are specific to both species groups and species, whereas size and body shape behaved conservatively and changed very little. However, some plesiomorphic character states of the aedeagus are still found in the basal group *Micranops*, such as the remarkable ventro-median lobe (Figs. 4, 5) which was considered as representing the parameres by Herman (1965a, b), and the short distal lobes of the median lobe.

Classification

In the West Palaearctic, Scopaeina sensu Coiffait (1982) comprises the genera *Micranops* and *Scopaeus* only. The monotypical genus *Coecoscopaeus*, established for *Scopaeus coecus* Peyerimhoff, 1906 from Tunisia, is here excluded from Scopaeina. Even though Coiffait (1984) placed this genus near *Scopaeus* according to the narrow neck, a character which, however, occurs in further paederines as well, he doubted his own classification. In adding *Coecoscopaeus coecus* to Scopaeina, Coiffait (1984) formed an obvious polyphyletic grouping. *Coecoscopaeus coecus* is a rather large (5 mm), light brown, depressed, flightless and anophthalmous paederine species with bilobed labrum, very sparsely and coarsely punctate, with a shining surface and a very simple, primitive aedeagus.

The present phylogenetic analysis gives specific reasons for *Scopaeus* and *Micranops* to be distinct groups. Besides the convincing apomorphies (see chapter "Results"), *Micranops* lacks the remarkable distal lobes of the aedeagus of *Scopaeus*. *Micranops* was erected by Cameron (1913) for the Jamaican species *M. brunneus* Cameron. Later, Coiffait (1981) established *Microscopaeus*, a junior synonym of *Micranops* (Herman, pers. comm.), as a subgenus of *Scopaeus* and designated *S. microphthalmus* Eppelsheim (= *Micranops pilicornis* (Baudi)) as the type species. *Nivorus* Herman, 1965, established as a subgenus of *Orus* Casey (genotype: *O. cameroni* Blackwelder), is also a junior synonym of *Micranops* (Herman, pers. comm.). *Micranops* was not noticed by recent authors. Fagel (1973), however, had already picked up the group as a distinct genus for the Afrotropical members according to the setigerous furrow behind the eyes (Fig. 1b), but he erroneously used the name *Geoscopaeus*, which was introduced by Coiffait (1960) as replacement name for the preoccupied name *Stilpon* Coiffait, 1952, established as a subgenus of *Scopaeus* with *S. baudrimonti* (= *S. ryei*) as the genotype (see also Coiffait 1984). *Geoscopaeus* is a junior synonym of *Scopaeus*.

The various subgenera which Coiffait (1952, 1960, 1968, 1981, 1984) described for West Palaearctic *Scopaeus* proved to be polyphyletic, except for *Hyperscopaeus*. Coiffait's subgeneric concept is quite absurd and mostly based on unsuitable features. He combined unrelated species in a subgenus or even placed the same species in different subgenera. For instance, *Anomoscopaeus*, established for West Palaearctic species of the *S. gracilis* group (Coiffait 1968), includes also *S. rubidus* which in fact belongs to the *S. sulcicollis* group. Likewise, Coiffait (1968) combined species of the *S. minutus* group with members of the *S. longicollis* group as subgenus *Alloscopaeus*.

Hyperscopaeus, described as a subgenus of *Scopaeus* by Coiffait (1984), differs strongly from *Scopaeus* s. str. and might be considered a distinct genus according to many external and sexual apomorphies (see chapter "Results"). A final classification of *Hyperscopaeus* within Scopaeina, however, should be left to an overdue generic revision of paederines.

Subgenus *Polyodontus* Solier, 1849 was established for the Chilean *S. angustatus* Solier. This preoccupied name (Coiffait 1968) was widely used for *Scopaeus* species with trapezoidal heads (e.g. Coiffait 1952, Mulsant & Rey 1878). As the genotype, *S. angustatus*, was described only from one female specimen (Coiffait 1960, 1968), the position of this subgenus, which with little doubt does not occur in the West Palaearctic, is doubtful. A phylogenetically founded subgeneric structuring of *Scopaeus* is not possible at the present state of taxonomic knowledge and requires a worldwide study.

Scopaeus bifossicapitata, an anophthalmous, endogeal Canarian species, differs considerably from *Scopaeus* according to the lack of the two-piece spermatheca and the presence of a strong, setiferous postocular furrow. The latter character refers rather to *Micranops*, but *S. bifossicapitata* is remarkably larger (3.5 mm), and the spermatheca is completely different. A final classification is impossible without knowledge of male characters.

Judging from the results of the present cladistic analysis, we propose the following supraspecific classification for the Scopaeina of the West Palaearctic, including new synonymies of supraspecific names (see also Appendix 2; Electr. Suppl. 02–02, Pt 1):

1. Genus *Micranops* Cameron, 1913
Nivorus Herman, 1965: 119, described as subgenus of *Orus* Casey; type species: *Orus cameroni* Blackwelder, 1943 (= *Micranops cameroni* (Blackwelder, 1943)); **syn. n.**
Microscopaeus Coiffait, 1981: 19, described as subgenus of *Scopaeus*; type species: *S. microphthalmus* Eppelsheim, 1888 (= *Micranops pilicornis* (Baudi, 1869)); **syn. n.**

2. Genus *Scopaeus* Erichson, 1840
Scopaeus Erichson, 1840: 604; type species: *Paederus laevigatus* Gyllenhal, 1827, designated by Duponchel (1841: 57).
Geoscopaeus Coiffait, 1960: 284; replacement name for *Stilpon* Coiffait, 1952: 6 (nec *Stilpon* Loew, 1859); type species: *S. baudrimonti* Coiffait, 1952 (= *S. ryei* Wollaston, 1872); **syn. n.**
Hyposcopaeus Coiffait, 1960: 285; type species: *S. scitulus* Baudi, 1857 (= *S. debilis* Hochhuth, 1851); **syn. n.**
Heteroscopaeus Coiffait, 1960: 285; type species: *S. sericans* Mulsant & Rey, 1854; synonymized with *Hyposcopaeus* Coiffait, 1960 by Coiffait (1968: 418).
Alloscopaeus Coiffait, 1968: 414; replacement name for *Euscopaeus* Coiffait, 1960: 285 (nec *Euscopaeus* Sharp, 1886: 548); type species: *S. didymus* Erichson, 1840; **syn. n.**
Anomoscopaeus Coiffait, 1968: 426; type species: *S. gracilis* (Sperk, 1835); **syn. n.**
Hyperscopaeus Coiffait, 1984: 148; type species: *Scopaeus spathiferus* Coiffait, 1970: 106.

The New World genus *Orus* Casey, 1884 was not examined for this study. However, judging from the revision by Herman (1965a, b), *Orus* appears closely related to *Micranops* according to the characteristic shape of the emargination of the male abdominal sternite 8 (Fig. 31), and to the general shape of the aedeagi (Figs. 4–6), which agree in the hook-shaped postforamen and the remarkable, ventro-medial lobe (parameres sensu Herman 1965a, b) and the short distal lobes. *Orus* is also linked with both *Scopaeus* and *Micranops* according to the two-piece spermatheca which, however, lacks the additional process of the chamber, here considered an apomorphy of *Scopaeus* s. str. According to Herman (1965a, b), *Orus* is distinguished from *Scopaeus* by the wider neck, which is at least as wide as one quarter of the head, but not from *Micranops* the neck of which is just as wide (Fig. 1a). This character, however, seems to be of little value for distinguishing these genera (Herman, pers. comm.). The phylogenetic relationships between *Micranops*, *Orus* and *Scopaeus* remain unclear pending a future generic revision of Paederinae.

Besides the supraspecific classification of the Scopaeina, the revision of species group names of *Scopaeus* resulted in further nomenclatorial changes and synonymies, as presented below. For full synonymies of the respective species and for biogeographical information see the species catalogue (Appendix 2; Electr. Suppl. 02–02, Pt 1).

***Scopaeus crassipes* Wollaston, 1867**: 242; syntypes: 2 males, 5 females, Cape Verde Islands (BMNH); 1 male, Cape Verde Islands, Brava (HECO).
S. tassiliensis Jarrige, 1958; holotype male, Algeria, Tassili n'Ajjer (MNHN); **syn. n.**
S. mauretanicus Coiffait, 1960: 289; holotype male, Mauritania, Rgueibat Temba (MNHN); **syn. n.**
Comments: The syntypes of *S. crassipes* from the BMNH and the HECO collections were examined as well as the holotypes of *S. mauretanicus* and *S. tassiliensis*. The latter are conspecific to *S. crassipes* according to the matching aedeagi, and here synonymized.

***Scopaeus didymus* Erichson, 1840**: 606; lectotype male, Italy, Sardinia (ZMHB); here designated.
S. mateui Coiffait, 1953: 268; holotype male, Spain, Almeria, Albanchez (MNHN); **syn. n.**
Comments: The lectotype of *Scopaeus didymus* is designated because the original type series was mixed; the other of the two former syntypes from Sardinia (ZMHB) is a male of *S. lanceolatus*. The lectotype is labeled as follows: "Sardinien Gena T. (handwritten) / 6353 / didymus Er (handwritten) / Zool. Mus. Berlin / Type / Lectotypus *Scopaeus* Erichson 1840 *didymus* Erichson 1840 / des. J. Frisch 2002".
The description of *S. mateui* Coiffait is based on specimens of *S. didymus* from southern Spain, the aedeagi of which have somewhat wider apical lobes than those of specimens from northern parts of the range, but in Spain both forms of the aedeagus are linked by transitional forms.

***Scopaeus nigellus* Wollaston, 1864**: 585; holotype female, Canary Islands, Gomera (BMNH); synonymized with *S. minimus* by Fauvel (1902: 86), here revalidated (**stat. n.**).
Comments: *Scopaeus nigellus* is not a synonym of *S. minimus*, because the spermatheca of the female holotype differs distinctly from that of *S. minimus*, which was illustrated by Frisch (1998). Moreover, because

S. minimus is unknown from South-West Europe and North Africa (Frisch 1998), occurence on the Canary Islands is very unlikely.

***Scopaeus perroti* Ochs, 1955**: 65; holotype male, Algeria, El Djazair (MHNG); **stat. n.**
Comments: *Scopaeus perroti* was described as a subspecies of *S. mitratus*. It is here elevated to species rank according to the different shape of the aedeagus.

***Scopaeus portai* Luze, 1910**: 393; lectotype male, Italy, Umbria, Porta (NHMW), designated by Frisch (1997c: 534).
S. bordei Peyerimhoff, 1914: 249; holotype female, Algeria, Biskra, Hamam-Salahin (MNHN); **syn. n.**
Comments: According to the shape of the spermatheca and the slender protarsomeres (see Frisch 1997c), the female holotype of *S. bordei* Peyerimhoff belongs to the yellowish-brown form of *S. portai* Luze from southern North Africa, from where Coiffait (1970) described *S. portai marocanus*. Frisch (1997c) synonymized *S. portai marocanus* because there is no difference regarding the shape of the aedeagus.

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Appendices °

Appendix 1: List of characters used for the cladistic analysis of West Palaearctic Scopaeina
Appendix 2°: Synonymic catalogue of West Palaearctic Scopaeina, including biogeographic information
Appendix 3°: Data matrix of characters used for the cladistic analysis
Appendix 4°: NONA file for phylogenetic analysis

° For Appendices 2 to 4 see Parts 1 to 3 of the Electronic Supplement at **http://www.senckenberg.de/odes/02-02.htm**

Appendix 1

List of the 76 external morphological and primary sexual characters used for the phylogenetic analysis of West Palaearctic species of Scopaeina.

1 – Width of neck (measured at hind margin of head) – 0: about one third of head width; 1: from one fourth to one fifth (Figs. 1a, 3); 2: about one eighth of head width (Fig. 2).
2 – Pronotum – 0: trapezoid, foreangles distinct; 1: parallel, foreangles rounded (Fig. 2); 2: tapering towards fore and hind margins, foreangles indistinct (Figs. 1a, 3).
3 – Labrum – 0: bidentate, laterally rounded; 1: quadridentate (Figs. 1a, 2, 3).
4 – Setigerous postocular furrow – 0: absent (Figs. 2, 3); 1: present (Figs. 1a, b).
5 – Surface – 0: dull, finely and densely punctate, microsculpture distinct; 1: shining, sparsely punctate, microsculpture indistinct.
6 – Head – 0: elongate, tempora parallel, hind margin distinctly concave (Fig. 2); 1: tempora parallel or slightly tapering, hind margin straight or somewhat convex (Fig. 1a); 2: more or less trapezoid, hind margin straight or somewhat concave, slightly vaulted; 3: parallel or somewhat trapezoid, hind margin straight, notably vaulted (Fig. 3).
7 – Eye length – 0: less than 0.7 of temporal length (Figs. 1a, 2, 3); 1: at least 0.7 of temporal length.
8 – Protarsomeres – 0: slightly elongate; 1: slightly transverse (Fig. 1a); 2: about twice as wide as long (Fig. 3); 3: three times as wide as long (Fig. 2).
9 – Mesotibiae – 0: slender, at least five times as long as wide (Figs. 1a, 2, 3); 1: dilated, not more than five times as long as wide.
10 – Tibiae – 0: without; 1: with long, black setae.
11 – Distal antennomeres – 0: distinctly elongate; 1: slightly elongate; 2: square or transverse (Figs. 1a, 2, 3).
12 – Distal antennomeres – 0: with; 1: without long setae.
13 – Spermatheca – 0: in one piece (Fig. 22); 1: composed of two pieces (Figs. 23–29).
14 – Spermathecal duct – 0: very long, winding; 1: very long, winding, ending in bursa (Fig. 27); 2: short, ending in bursa (Fig. 24); 3: rather short, sclerotized section with terminal thickening (Fig. 26); 4: very short, sclerotized section with terminal thickening (Fig. 28); 5: very short, without thickening at transition to hyaline section.
15 – Bursa of spermathecal duct – 0: absent; 1: large (Figs. 24, 27, 30); 2: small, strongly sclerotized; 3: small, weakly sclerotized.
16 – Chamber of spermatheca – 0: without process (Fig. 22), evenly tapering towards spermathecal duct (Fig. 23); 1: with process (Figs. 24–29).
17 – Two-piece spermatheca – 0: absent (Fig. 22); 1: different; 2: stout, portions strongly flexed, chamber small, spermathecal duct strong and flexed up at right angle; 3: large, portions weakly flexed (Fig. 27); 4: with chamber notably lengthened (Fig. 25); 5: with chamber having a short, additional canal (Fig. 29); 6: with portions strikingly short; 7: small, portions little flexed, process dentate terminally.
18 – Sternite 8 of female – 0: not emarginate; 1: emarginate terminally.
19 – Laterotergite 9, apex – 0: bidentate; 1: unidentate, with dorsal emargination marked by a tooth or angle (Figs. 37–39).
20 – Laterotergite 9, dorsal emargination – 0: absent; 1: large, marked by a strong tooth (Fig. 37); 2: small, marked by a strong tooth (Fig. 38); 3: small, marked by a small tooth; 4: small, without tooth (Fig. 39); 5: large, without tooth.
21 – Male sternite 7, hind margin – 0: straight or slightly concave; 1: with some short, thick median setae; 2: with deep, rectangular emargination.
22 – Male abdominal sclerites – 0: regularly setose; 1: sparsely setose.
23 – Male sternite 8, hind emargination – 0: triangular (Fig. 34, 36); 1: short, semicircular; 2: small, narrow, triangular (Fig. 31); 3: narrow, deep, proximally round, surrounded by an outer margin extended into two distal teeth (Fig. 35); 4: short, wide, with a median, triangular emargination; 5: wide, very deep, proximally round; 6: short, wide (Fig. 33); 7: very deep but narrow (Fig. 32); 8: short, lateral margins wave-like convex.
24 – Male sternite 8, triangular emargination – 0: absent; 1: up to one fourth of sternite 8 length; 2: acute proximally, at least one third of sternite 8 length (Fig. 34); 3: up to one fourth of sternite 8 length, sternite with distinct median ridge and asetose, lateral planations; 4: one third of sternite 8 length, sternite with distinct median ridge and lateral, asetose planations (Fig. 36); 5: up to one fourth of sternite 8 length, sternite with densely setose median ridge and lateral, little-setose planations; 6: up to one fourth of sternite 8 length, sternite with median ridge setose terminally and with lateral, setose planations; 7: with convex lateral margins and a very acute apex.
25 – Male sternite 8, short, wide emargination – 0: absent; 1: almost semicircular; 2: with slightly convex middle, without median setae (Fig. 33).
26 – Aedeagus – 0: with short, distinct apical lobes and dorsal lobe (Figs. 4–6); 1: with unipartite, rather membranous apical portion of median lobe (Figs. 7–9); 2: with well-developed, large apical lobes and dorsal lobe (Figs. 10–21).
27 – Flagellum of aedeagus – 0: surrounded by denticles or teeth (Figs. 7–9); 1: without additional structures (Figs. 4–6, 10–21).

28 – Flagellum of aedeagus – 0: flagellate, surrounded by denticles and teeth (Figs. 7–9); 1: stout, with denticles; 2: stout, without denticles (Figs. 4–6); 3: flagellate, without additional structures (Figs. 10–21).
29 – Flagellum of aedeagus – 0: bearing some ventral denticles (Fig. 16); 1: filiform terminally, strongly projecting from apical lobes; 2: asymmetical, at least as long as apical lobes (Figs. 13–15); 3: strikingly short; 4: with ventrally curved apex; 5: somewhat thickened but at about its half length tapering and flexed ventrally; 6: bearing apical teeth (Figs. 19, 20); 7: strong, knife-shaped, reaching; 8: strong, shortly tapering at apex, reaching apices of apical lobes; 9: strong, shortly tapering at apex, not reaching apices of apical lobes (Figs. 10, 11).
30 – Flagellum of aedeagus with apical teeth – 0: absent; 1: S-shaped, orientated longitudinally (Fig. 19); 2: evenly curve ventrally.
31 – S-shaped flagellum of aedeagus – 0: absent or different; 1: as long as dorsal lobe (Fig. 19).
32 – Asymmetric flagellum of aedeagus – 0: absent; 1: without basal tooth; 2: with, in ventral view, right basal tooth (Fig. 14).
33 – Ventro-median process of median lobe – 0: absent (Figs. 7–21); 1: present (Figs. 4–6).
34 – Ventral process of phallobase – 0: absent (Figs. 4–6, 10–21); 1: long, rod-shaped (Figs. 7–9); 2: very short, obtusely rounded; 3: lamelliform; 4: short, rod-shaped.
35 – Ventral endophallic process – 0: absent (Figs. 7, 8); 1: present (Figs. 4, 5, 10–21).
36 – Ventral endophallic process – 0: absent (Figs. 7, 8); 1: lobiform, as long as apical lobes (Figs. 4, 5); 2: small, stout (Fig. 14); 3: disc-shaped or almost triangular (Figs. 16, 17); 4: short, acute, semicircularly curved; 5: flagelliform (Figs. 19, 20); 6: long, hook-shaped; 7: curved with emarginate apex; 8: long, hook-shaped with emarginate apex; 9: short, hook-shaped (Fig. 10).
37 – Small, stout ventral endophallic process – 0: absent, 1: extremely small, invisible in lateral view (Fig. 14); 2: visible in lateral view; 3: acute, triangular.
38 – Flagelliform ventral endophallic process – 0: absent; 1: hook-like, flexed to the right in ventral view (Fig. 20); 2: slender, more or less hook-shaped, little curved in ventral view.
39 – Lateral lobes – 0: absent (Figs. 19–21); 1: reduced, each marked by two groups of setae; 2: each bearing an apical group of long setae (Figs. 16–18); 3: large, each with two groups of setae; 4: large, strongly projecting, with numerous ventral setules; 5: weakly sclerotized, without setae; 6: reduced, obtuse, each bearing a group of about five ventrally pointing setae (Figs. 10–12); 7: absent, each indicated by a ventral group of long setae (Figs. 13–15); 8: of unequal length, bearing long apical setae; 9: obtuse, each bearing a line of setae invisible in dorsal view.
40 – Lateral lobes with apical group of long setae – 0: absent; 1: short but wide, setae each forming a ventral line; 2: elongate, apex acute; 3: short, very wide, bearing some short additional ventral setae; 4: pointing ventrally; 5: curved laterally, with groups of long setae; 6: with setae half as long as apical lobes; 7: short, setae long (Figs. 16–18).
41 – Lateral lobes with setules – 0: absent or different; 1: moderately developed.
42 – Dorsal lobe – 0: indistinct (Figs. 7–9); 1: distinct (Figs. 4–6, 10–21).
43 – Dorsal lobe – 0: different; 1: large, weakly sclerotized (Figs. 4–6); 2: more or less elongate, strongly sclerotized (Figs. 7–21).
44 – Dorsal lobe – 0: different; 1: bearing long inner setae (Figs. 5, 6).
45 – Dorsal lobe – 0: different; 1: without distal emargination or ventral teeth; 2: emarginate or bilobed at apex, without distinct ventral teeth (Figs. 16, 18); 3: emarginate or not, with various ventral teeth (Figs. 19–21); 4: strongly enlarged, bilobed; 5: asymmetrical (Figs. 13–15); 6: stout, bearing two apical teeth; 7: with distinct apical portion; 8: vestigial (Figs. 10, 12); 9: deeply emarginate, apical teeth strongly curved towards phallobase.
46 – Distinct apical portion of dorsal lobe – 0: absent; 1: emarginate at apex, bearing two pairs of ventral teeth and two ventral lamellae; 2: convex at apex, without ventral teeth.
47 – Bidentate dorsal lobe – 0: absent or different; 1: with two ventral teeth.
48 – Bidentate apical portion of dorsal lobe – 0: absent or different; 1: with widely separate apical teeth.
49 – Emarginate dorsal lobe – 0: absent; 1: short, triangular; 2: slender (Figs. 16, 18).
50 – Triangular dorsal lobe – 0: absent; 1: with, in lateral view, wide, convex apical teeth; 2: with, in lateral view, slender, stout apical teeth.
51 – Short triangular dorsal lobe – 0: absent; 1: deeply emarginate, with separate apical teeth; 2: slightly emarginate.
52 – Long triangular dorsal lobe – 0: absent or different; 1: emarginate in distal half, distal teeth separate; 2: emarginate in distal half, distal teeth adjacent; 3: with diverging distal teeth (Figs. 16, 18).
53 – Diverging teeth of triangular dorsal lobe – 0: different; 1: with (Figs. 16, 18); 2: without apical teeth or denticles.
54 – Dorsal lobe – 0: different; 1: half as long as apical lobes, bearing two short, ventrally curved apical teeth; 2: little emarginate at apex, bearing different teeth; 3: deeply emarginate, extended into two ventrally curved teeth of unequal length (Figs. 19–21); 4: extended into a long tooth; 5: claviform in lateral view.
55 – Dorsal lobe – 0: different; 1: with three ventral teeth; 2: with two ventral teeth.
56 – Dorsal lobe – 0: different; 1: with lobiform apical teeth (Fig. 19).
57 – Apical lobes – 0: distinct from median lobe at very apex (Figs. 7, 8); 1: distinct (Figs. 4–6, 10–21).
58 – Distinct apical lobes – 0: absent; 1: short, lobiform, about parallel, not enlarged apically (Figs. 4–6); 2: of different shape, but apically enlarged (Figs. 10–21).

59 – Distinct apical lobes – 0: different or absent; 1: each with distinct, triangular distal portion; 2: knife-shaped (Figs. 16–18); 3: very short, angled, flexed ventrally (Figs. 10–12); 4: with inner row of setae; 5: asymmetrical (Figs. 13–15); 6: conspicuously shorter than dorsal lobe; 7: simple, convex ventrally, widening laterally; 8: ventrally curved with longitudinally curved, round apex; 9: convexly enlarged ventrally, each with distinct, membranous apical portion.
60 – Distinct distal portions of apical lobes – 0: absent; 1: weakly distinct; 2: well distinct in lateral view.
61 – Distinct distal portions of apical lobes – 0: absent; 1: fused; 2: distinct.
62 – Distinct distal portions of apical lobes – 0: absent; 1: with parallel; 2: with triangular inner ventral margins.
63 – Distinct distal portions of apical lobes – 0: absent; 1: with widening outer ventral margins.
64 – Distinct distal portions of apical lobes – 0: absent; 1: with inner ventral margins each forming a right angle.
65 – Knife-shaped apical lobes – 0: absent; 1: very slender, each with shallow emargination; 2: slender, widened distally, each with deep emargination and dorsally upturned apex; 3: with deep, narrow or semicircular emargination, apex dorsally upturned; 4: with very wide emargination, distal halves straight; 5: without emargination (Figs. 16–18).
66 – Apex of knife-shaped apical lobes – 0: apical lobes different; 1: evenly tapering (Figs. 16–18); 2: upturned; 3: knife-shaped.
67 – Apical lobes – 0: without long setae; 1: with long, lateral or ventral setae.
68 – Apical lobes with inner row of setae – 0: absent; 1: short, almost symmetrical; 2: different, slightly asymmetrical.
69 – Asymmetrical apical lobes – 0: absent; 1: long and slender (Figs. 13–15); 2: shorter, strongly asymmetrical.
70 – Apical lobes – 0: different; 1: with laterally enlarged, ventrally emarginate apical portion (Figs. 19–21).
71 – Apical lobes with enlarged apical portion – 0: absent; 1: slender, emargination shallow (Fig. 19); 2: hook-shaped distally.
72 – Sclerotized ring of phallobase – 0: absent (Figs. 4–6); 1: present (Figs. 7–21).
73 – Sclerotized ring of phallobase – 0: absent (Figs. 4–6); 1: rather broad; 2: broad, ventrally enlarged, lateral portions rather slender; 3: slender, lateral portions transverse and widely separate in dorsal view; 4: broad, lateral portions strong, separate in dorsal view; 5: broad, lateral portions widely separate in dorsal view (Figs. 13–15); 6: broad, with two close lateral portions in dorsal view; 7: broad, with longitudinal lateral portions separate from lateral margins of aedeagus (Figs. 10–12); 8: very narrow and widening ventrally, lateral portions slender (Figs. 16–18, 19–21); 9: striking, broad (Figs. 7–9).
74 – Lateral ridges of median foramen – 0: absent (Figs. 4, 5); 1: short, little sclerotized; 2: about half as long as phallobase, strongly sclerotized.
75 – Median foramen – 0: at distal end of phallobase; 1: near round end of phallobase; 2: different.
76 – Lateral lobes – 0: absent (Figs. 4–9); 1: absent, indicated by not more than a few setules (Figs. 19–21); 2: present (Figs. 10–18).